

SOME EARTHWORMS FROM THE WET TROPICS AND FROM BUNYA MOUNTAINS, QUEENSLAND (MEGASCOLECIDAE: OLIGOCHAETA)

B.G.M. JAMIESON

Jamieson, B.G.M. 1994 12 01: Some earthworms from the Wet Tropics and from Bunya Mountains, Queensland (Megascolecidae: Oligochaeta). *Memoirs of the Queensland Museum* 37(1): 157-180. Brisbane. ISSN 0079-8835.

A systematic study, supported by a cladistic analysis, indicates that North Queensland species of *Diporochoeta* warrant separate generic status, as *Terrisswalkerius* gen. nov. *Fletcherodrilus* gen. nov. represents an apomorphic clade of this assemblage which is, nevertheless, retained as a separate genus. The Bunya Mountains isolate of *Diporochoeta* merits separate generic status, as *Hiatidrilus bunya*, and *Cryptodrilus semicinctus*, from Grafton, on the Clarence River, New South Wales, is congeneric with it. The residue of *Diporochoeta* is a paraphyletic and polyphyletic entity requiring further resolution. The cladistic analysis also investigates wider relationships of the above genera with the remainder of the Perionychini. In the analysis the type-species of *Diporochoeta*, *D. intermedia*, is separated by other genera from those *Diporochoeta* species here assigned to *Terrisswalkerius* and, indeed, from all other included *Diporochoeta* species. The analysis suggests that *Perionychella*, currently subsumed in *Diporochoeta*, is the sister-taxon of the *Terrisswalkerius-Fletcherodrilus* assemblage. The phylogram is not inconsistent with the generic status of the remaining perionychin genera *Graliophilus*, *Heteroporodrilus*, *Paraplutellus*, *Perionychella*, *Pinguidrilus*, *Plutellus*, *Pseudoperichaeta*, *Simsia*, and *Woodwardiella* but significant autapomorphies remain to be established for some of these. Within *Terrisswalkerius* the most plesiomorphic species appears to be *T. blounti*. *T. atavius*, is the most derived species and forms the sister-taxon of *Fletcherodrilus*. Pairs of sister-species are: *T. grandis* and *T. terraereginae*, *T. millaamillaa* and *T. mcdonaldii* sp. nov., *T. ather-tonensis* and *T. oculus*, *T. kuranda* and *T. canaliculatus*, and *T. nashi* and *T. liber* sp. nov. A monophyletic, though weakly defined, species group contains *T. ather-tonensis*, *T. oculus*, *T. canaliculatus*, *T. kuranda*, *T. crateris*, *T. nashi* and *T. liber*. The new species *T. covacevichae* and *Fletcherodrilus menurus* are also described. □ *Terrisswalkerius* gen. nov., *Hiatidrilus* gen. nov., *Fletcherodrilus*, *Diporochoeta*, *Perionychini*, cladistics.

B.G.M. Jamieson, Zoology Department, University of Queensland, Brisbane, Queensland 4072, Australia; 28 August 1994.

Diporochoeta was erected by Beddard (1890) with, as its type-species, the New Zealand species *Diporochoeta* (= *Perichaeta*) *intermedia* Beddard, 1889. Prior to the present work, *Diporochoeta* contained 78 Australian species. These species had been initially placed, on erection, in some eight genera in addition to *Diporochoeta*. Of these, five (*Cryptodrilus*, *Megascolex*, *Megascolides*, *Perionyx*, *Plutellus*) are still recognised as distinct genera, two (*Perionychella* and *Vesiculodrilus*) have been subsumed in *Diporochoeta* (see Jamieson, 1976b) and one (*Perichaeta*) in *Megascolex* (see Michaelsen, 1900). Here evidence will be presented, in a cladistic analysis, in support of removal on 'intuitive' grounds, of 16 species from North Queensland from *Diporochoeta* and their transfer to a new genus, *Terrisswalkerius*, and for transfer of two species to a further new genus, *Hiatidrilus*. The number of Australian species of *Diporochoeta* is thus reduced to 60.

Three new species are added to *Terrisswalkerius*. The status and phylogenetic affinities of *Fletcherodrilus* will also be investigated. Jamieson (1976b) observed that little other than the unpaired genital pores warranted separation of *Fletcherodrilus* from *Diporochoeta*, that inclusion in the latter genus as a subgenus would be sustainable, and that *Fletcherodrilus* may be regarded as the apomorph sister-group of *Diporochoeta*. A new species is added to *Fletcherodrilus*. Erection of a distinct genus for north Queensland species of *Diporochoeta* and the apomorphic status of *Fletcherodrilus* have been independently suggested by Dyne & Wallace (1994).

The status of the predominantly Western Australian genus *Graliophilus* Jamieson, 1971b, was rendered uncertain by addition of North Queensland species to *Diporochoeta* by Jamieson (1976b) which blurred the distinction between the two genera. *Graliophilus* was

retained by Jamieson (1974a) on the grounds, inter alia, that in Western Australian species the number of spermathecae was less (2 or 3 pairs) than the five pairs usual in *Diporochoaeta* and that the avesiculate nephridia and totally lumbricin condition of the setae were constant whereas the combination of these characters was known in only one species of *Diporochoaeta* from eastern Australia (Tasmania). It was concluded, however, that the low phenetic resemblance between *Diporochoaeta* and *Graliophilus* demonstrated by Wallace (1972) and the very distinct morphology of some *Graliophilus* species suggested that this genus should be retained. The present study examines cladistic relationships of *Graliophilus* to *Diporochoaeta* s. lat. and includes in the analysis the type-species of all named genera of the Perionychini, viz. the 13 genera *Diporochoaeta*, *Fletcherodrilus*, *Graliophilus*, *Heteroporodrilus*, *Hiatidrilus*, *Paraplutellus*, *Perionychella*, *Pinguidrilus*, *Plutellus*, *Pseudoperichaeta*, *Simsia*, *Terrisswalkerius*, and *Woodwardiella*.

Retention of *Perionychella*, for forms lacking nephridial bladders (and possibly with racemose prostates, as in the type-species) as a subgenus of *Diporochoaeta* deserves consideration but was not upheld (Jamieson, 1976b) as the distinction between an avesiculate and a vesiculate group of species had become increasingly blurred. Thus Tasmanian *Diporochoaeta murtoni* has avesiculate and, typically, vesiculate individuals (Jamieson, 1974a). *D. grandis* has vesiculate and avesiculate populations, or even segments in the same individual and in *D. terraereginae* (both are Queensland species) nephridial ducts are transitional between the two conditions. Perhaps more significantly, in an unpublished taxonomic (numerical) study vesiculate and avesiculate species formed mixed groups, especially where all nephridial characters are omitted. It is noteworthy that Michaelsen, who ignored the presence or absence of bladders, considered the avesiculate *D. atavia* to be merely a form of the vesiculate *D. athertonensis*, a decision indicating the closeness of the entities with the antithetic conditions, notwithstanding the view (Jamieson, 1976b) that they are distinct species.

Unless otherwise stated material studied is housed in the Queensland Museum (QM).

Terrisswalkerius gen. nov.

DIAGNOSIS

Setae numerous (>14) per segment. Genital markings other than porophores bearing the

female, male and spermathecal pores, absent. A pair of combined pores of vasa deferentia and tubular or tubuloracemose prostates on XVIII. Last hearts in XII or XIII. Gizzard in V or VI (or VII?) (well developed); intestinal caeca and typhlosole absent. Extramural calciferous glands absent. Nephridia stomate exonephric holonephridia with or without bladders; their pores in straight or sinuous lines but never with regular alternation. Spermathecae 1 to 5 pairs, rarely unpaired midventral, pre-testicular, diverticulate; diverticulum usually single, uniloculate; rarely double, rarely multiloculate.

DESCRIPTION

Terrestrial worms. Form circular in cross section or less commonly slightly depressed dorsoventrally; anus terminal. With or without pigmentation. Prostomium proepilobous to tanylobous. Body usually with a dorsal groove (canalicula) in part or the whole of its length. Dorsal pores present; in 3/4 - 6/7, usually 5/6. Setae perichaetine throughout. Nephridia in single lateral series throughout, or in irregularly sinuous series, varying from far dorsally to far ventrally but never showing regular alternation. Posterior limit of the clitellum shortly anterior to the male pores or including these. A pair of male pores on XVIII, each pore the combined opening of a prostate gland and the corresponding vasa deferentia. Female pores paired on XIV. Spermathecal pores 1 to 5 pairs, rarely unpaired midventral, between intersegmental furrows 4/5-8/9, rarely shortly behind the intersegments.

Dorsal blood vessel single, continuous onto the pharynx; last hearts in XII or, rarely, XIII; hearts in X posteriorly latero-oesophageal, each receiving a connective from the supra-oesophageal vessel and a lesser connective (sometimes absent?) from the dorsal vessel. Supra-oesophageal vessel restricted to the post-gizzard oesophagus, moderately to well developed. Subneural blood vessel absent. Gizzard in V or, more frequently, VI (or VII?) (well developed). Extramural calciferous glands not developed but oesophagus vascularized and often internally rugose in some segments from VIII to XVI. Intestine commencing in XVI to XIX, most frequently XVII; intestinal caeca and typhlosole absent. Nephridia simple, exonephric holonephridia throughout; tufted nephridia absent; bladders usually present, with or without diverticula; exceptionally (*D. grandis*, part.) avesiculate in the forebody and vesiculate in the hindbody. Holandric (testes in X and XI); seminal vesicles two to four pairs, in IX

to XII, exceptionally (*T. terraereginae*) in VIII (in addition to IX and XII), and often with pseudovesicles in XIII. Metagynous (ovaries and funnels in XIII). Prostates tubular or tubuloracemose, never racemose. Penial setae absent. Spermathecae diverticulate; diverticulum usually single, uniloculate; rarely double or multiloculate.

DISTRIBUTION

The Wet Tropics of eastern North Queensland, from the Paluma Range, 19S., near Townsville, north to the Upper Endeavour River shortly below 15°S.

TYPE SPECIES

Terrisswalkerius (= *Perichaeta*) *canaliculatus* (Fletcher, 1887a); here selected because its anatomy is well known and it is the most widely distributed species of the genus and therefore the most likely to be available for molecular and other studies.

ETYMOLOGY

Named in memory of Terry Walker. Gender masculine.

INCLUDED SPECIES

T. atavius (Michaelsen, 1916); *T. athertonensis* (Michaelsen, 1916); *T. barronensis* (Fletcher, 1886b); *T. blounti* (Jamieson, 1976b); *T. canaliculatus* (Fletcher, 1887a); *T. covacevichae* sp. nov.; *T. crateris* (Jamieson, 1976b); *T. erici* (Michaelsen, 1916); *T. grandis* (Spencer, 1900); *T. kuranda* (Jamieson, 1976b); *T. liber* sp. nov.; *T. mcdonaldi* sp. nov.; *T. millaamillaa* (Jamieson, 1976b); *T. montislewisi* (Jamieson, 1976b); *T. nashi* (Jamieson, 1976b); *T. oculatus* (Jamieson, 1976b); *T. phalacrus* (Michaelsen, 1916); *T. raveni* (Jamieson, 1976b); *T. terraereginae* (Fletcher, 1890).

KEY TO SPECIES OF *TERRISSWALKERIUS*

- 1. Spermathecal pores 5 pairs, in or shortly behind intersegmental furrows 4/5-8/9 2
 - Spermathecal pores 1 to 4 pairs (rarely unpaired, midventral), in or shortly behind some or all of intersegmental furrows 5/6-8/9 4
 - Spermathecal pores 5 pairs
 - 2. Spermathecal pores in a lines. Spermathecal duct very short. Last hearts in XIII *T. grandis*

- Spermathecal pores median to a lines. Spermathecal duct long and slender though shorter than the ampulla. Last hearts in XII 3
- 3. Spermathecal pores of 8/9 c. 0.02 body circumference apart. Male pores c. 0.03 body circumference apart. Seminal vesicles in IX and XII. Nephridial bladders present *T. atavius*
 - Spermathecal pores of 8/9 c. 0.06 body circumference apart. Male pores c. 0.1 body circumference apart. Seminal vesicles in XI and XII (or absent). Nephridial bladders absent *T. phalacrus*
- 4. Spermathecal pores in 4 intersegments, 5/6-8/9 or 4/5-7/8, paired or single 5
 - Spermathecal pores 3 pairs or fewer 9

Spermathecal pores in 4 intersegments

- 5. Spermathecal pores in 5/6-8/9, unpaired, midventral *T. mcdonaldi* sp. nov.
 - Spermathecal pores 4 pairs, in 4/5-7/8 or 5/6-8/9 6
- 6. Spermathecal pores 4 pairs, in 4/5-7/8 *T. terraereginae*
 - Spermathecal pores 4 pairs, in 5/6-8/9 7
- 7. Male pores median to a lines, their papillae contiguous in the midline. Nephridial bladders absent *T. millaamillaa*
 - Male pores between setal lines a and d, their papillae well separated in the midline. Nephridial bladders present 8
- 8. Prostomium tanylobous, with wide dorsal tongue. Nephropores in a straight series on each side *T. erici*
 - Prostomium epilobous or proepilobous; with a deep middorsal groove which continues to the hind margin of the peristomium. Nephropores in an irregularly sinuous series, varying from far dorsally to far ventrally, on each side *T. kuranda*
- 9. Spermathecal pores 3 pairs, in 4/5-6/7 or in or shortly behind 6/7-8/9 10
 - Spermathecal pores 1 or 2 pairs, in some of 5/6-8/9 16

Spermathecal pores 3 pairs

- 10. Spermathecal pores 3 pairs, in 4/5-6/7 11
 - Spermathecal pores 3 pairs, in or shortly behind 6/7-8/9 13
- 11. Spermathecal diverticulum long and tortuous.
 - Spermathecal pores in the vicinity of d to e lines 12
 - Spermathecal diverticulum short and clavate.
 - Spermathecal pores between a and b lines *T. montislewisi* (part.)

12. Spermathecal diverticulum longer than ampulla plus duet. (Spermathecal pores in *d* lines) . . .
 *T. barronensis*
 Spermathecal diverticulum shorter than ampulla plus duet. (Spermathecal pores in *d-e* lines) . . .
 *T. raveni*
13. Male pores very close together, almost contiguous midventrally, on a common papilla . . .
 *T. athertonensis*
 Male pores well separated, between setal lines *b* and *f*, on a pair of papillae 14
14. Spermathecal diverticulum simple, shortly clavate 15
 Spermathecal diverticulum composite, consisting of as many as 4 parallel conjoined tubes with terminal, knoblike seminal chambers; approximately as long as the spermathec
 *T. oculatus*
15. Spermathecal pores varying from setal lines 3 to 5. Male pores between setal lines 4 to 7. Prostate glands restricted to XVIII . . . *T. canaliculatus*
 Spermathecal pores in *b* lines. Male pores in *ab*. Prostate glands concealing the gut, in XVIII-XXI *T. covacevichae* sp. nov.

Spermathecal pores 2 pairs

16. Spermathecal pores 2 pairs, in 5/6 and 6/7 . . .
 *T. montislewisi* (part)
 Spermathecal pores 1 pair, in 6/7 or 7/8 or 8/9 17

Spermathecal pores 1 pair

17. Spermathecal pores 1 pair, in 8/9. Spermathecal diverticulum long and tortuous 18
 Spermathecal pores 1 pair, in 6/7 or 7/8 . . . 19
18. Spermathecal pores in setal lines *c* to *d*.
 *T. nashi*
 Spermathecal pores well median of setal lines *a*
 *T. liber* sp. nov.
19. Spermathecal pores 1 pair in 6/7 . . . *T. crateris*
 Spermathecal pores in 7/8 *T. blounti*

Terrisswalkerius athertonensis (Michaelsen, 1916) comb. nov. (Figs 1; 2A,B)

- Perionyx (Diporochoaeta) athertonensis* Michaelsen, 1916: 7-9, pl.1, fig.7.
Diporochoaeta athertonensis; Jamieson, 1971c: 83; Jamieson, 1976b:14, figs 1, 9a, table 1.
Perionychella (Perionychella) athertonensis; Jamieson, 1974a: 221.

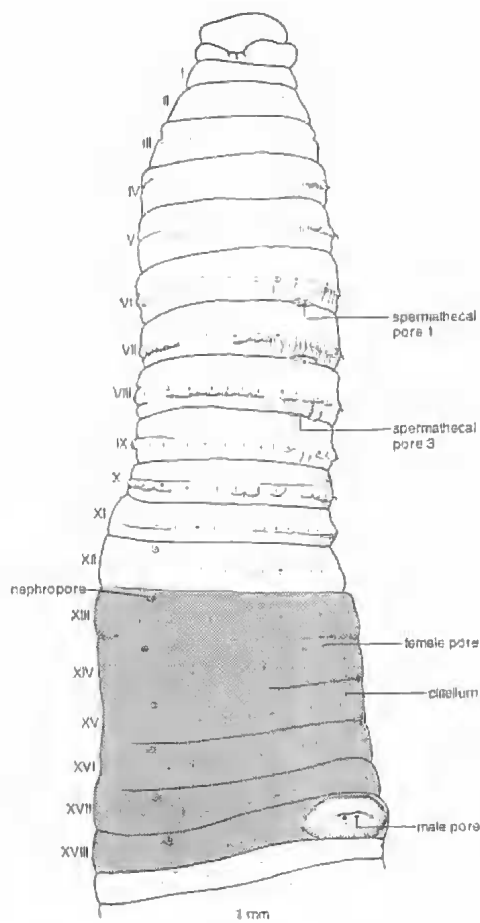


FIG. 1. *Terrisswalkerius athertonensis* (Michaelsen, 1916). Mt Lewis, QMG9210. Forebody and elitellar region, lateroventral view.

TYPE LOCALITY

17°16'S.145°29'E., Atherton. 15°39'-27°52'S.145°15'E.-15312'E., Cedar Creek. All Queensland.

MATERIAL EXAMINED

SYNTYPES: Zoology Museum Hamburg HMV8481 (re-examined), HMV8482 (now represented by soil debris only). Stockholm Museum NHRS1245.
 NEW RECORD: 16°34'S. 145°17'E., Mt Lewis, in rainforest, F. Little and Queensland Museum Party, 7 Nov 1975, a single, previously dissected, clitellate specimen, QMG9210. (This material was correctly identified by R. Raven as *Diporochoaeta athertonensis*, the first sighting since Michaelsen's 1916 description); 2 elitellate specimens, rainforest, 6kms from Malanda Falls Environmental Park, on road to Atherton, B.G.M.

Jamieson, 12. Dec 1994, QMG211454. All in Queensland.

DESCRIPTION

(The following account combines descriptions of all known material. The single specimen from Mt Lewis is a posterior amputee).

Length 36-68mm, width 3-5mm, segments 98-108. Pigmented violet brown, little colour remaining in Mt Lewis specimen. Tanylobous. Body canaliculate throughout. First dorsal pore 5/6. Setal circle regularly interrupted ventrally, dorsally irregularly; *a* lines regular throughout; *b* lines regular throughout or for much of body length; *c* lines less regular; in mid- and hind-body, *aa* = 1.5-2 *ab*; *dd* 1.3-2.3 *yz*, in anterior segments much larger. Intersetal spacing dorsally irregular and in general wider than ventrally, except in forebody. Setal numbers (Michaelsen): 10/II, 15/V, 22/VIII, 24/X, 36/XIX, 35/XXVI, 36/LXX, 38/LXXI; 23 in XII, 40 in LXXVI (Mt Lewis). Nephropores (see also internal description) visible as a straight series on each side, immediately ventral of setal lines 10 on clitellum. Clitellum annular, XIII-1/2XVIII, XVIII; intersegmental furrows, setae, nephridial and dorsal pores clearly visible or (Mt Lewis) dorsal pores occluded. Male pores scarcely visible, very near ventral midline, 0.11 - 0.2mm apart (Mt Lewis) in a transversely oval midventral glandular field. Female pores (Mt Lewis) a pair of minute points, shortly median of setae *a*, nearer anterior border than they are to setal arc of XIV. Spermathecal pores, hardly externally recognizable, 3 pairs, in 6/7-8/9, very near ventral midline, 0.05-0.07mm apart, or (Mt Lewis) 0.08mm and about one half *aa* apart. Genital markings absent.

Septa from 6/7 well developed, 6/7-8/9 thin, 9/10-12/13 slightly thickened, the remainder thin (type material). Dorsal blood vessel single; last hearts in XII; large and latero-oesophageal in X-XII. Gizzard large, in VI or (Mt Lewis) apparently V. Oesophagus in XII-XIV with folded, vascularized walls or (Mt Lewis) X-XVI vascularized; but lacking extramural calciferous glands and with no development of large paired blood vessels. Intestine commencing abruptly in XVI or (Mt Lewis) XVII; typhlosole and caeca absent. Nephridial bladders (not mentioned by Michaelsen), in the syntypes, wide tubes, those in II convoluted and discharging in *z* lines, succeeding bladders progressively more ventral so that by V they are in setal lines 7. Nephropores in 9 on XII, 8 on clitellum and 12 caudally. By V vesicles take form of a tube with an abrupt lateral bend at

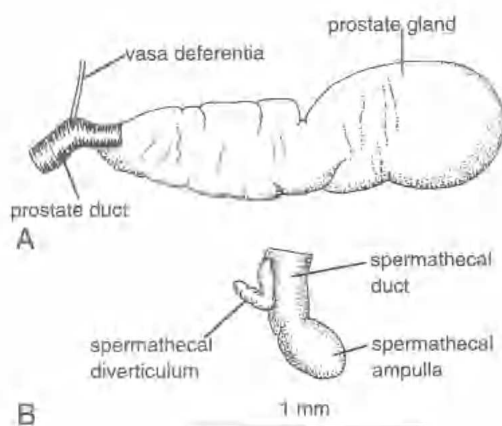


FIG. 2. *Terriswalkerius athertonensis* (Michaelsen, 1916). Mt Lewis, QMG9210. A, right prostate; B, right posterior spermatheca.

c. midlength, two limbs parallel, ectal limb wide and often bent near pore (V-shaped bladders). In anterior intestinal region ental limb has become so narrow that it can scarcely be considered part of bladder and is so closely adherent to ectal limb that bend has spurious appearance of a diverticulum. This form persists to caudal extremity and although ental limb widens slightly it remains much narrower than ectal limb. In Mt Lewis specimen nephridial postseptal portions commence in II and a large preseptal funnel is demonstrable for those of III and less certainly II; ducts of the first three pairs are dilated but questionably to be considered bladders; thereafter they form definite bladders; those of V are V-shaped and those of anterior intestinal region similarly conform with syntypes. Two pairs of iridescent sperm funnels in X and XI; racemose seminal vesicles in IX and XII (Mt Lewis). Prostates tubular, almost confined to XVIII (syntypes and Mt Lewis); central lumen (Michaelsen) simple, about one eighth width of gland; wall of gland with two layers of glandular cells overlain by peritoneum, cells of inner layer in groups around apparently lumenless axes. Duct (all specimens) well defined from gland; about one fourth as long, much thinner and muscular. The two vasa deferentia of a side running close together and joining prostate duct at its midlength before (Michaelsen) passing distally to fuse with its lumen shortly before distal end. Penial setae absent. Ovaries wide and bushy, oviducal funnels large; oviducts short and straight. Spermathecae 3 pairs; ampulla smooth, saclike or ovoid, ducts sharply demarcated, two thirds width of ampulla

and somewhat shorter or (Mt Lewis) approximately as long; a slender clavate to digitiform diverticulum, with simple lumen, entering duct in body wall or (Mt Lewis) near its base and shorter than ampulla plus duct.

REMARKS

The new material, from Mt Lewis, agrees closely with the type material in most respects, indicating conspecificity. The difference of one segment recorded in the position of the gizzard and intestinal origin between the type and Mt Lewis material is not, however, usual intraspecifically and requires confirmation from better preserved material if available.

Terrisswalkerius covacevichae sp. nov. (Figs 3; 4A,B)

TYPE LOCALITY

17°33'S.145°34'E., Mt Fisher, N.E. Queensland, J. Covacevich, V.E. Davies, R. Raven, 23.iv. 1978.

MATERIAL EXAMINED

HOLOTYPE: QMG211447 ex QMGH1991.

PARATYPE: QMG211448 ex QMGH1991.

DESCRIPTION

Length (holotype, H, is a posterior amputee), 125mm (paratype, P), width 5.0mm (P), 6.2mm (H); segments 222 (P). Body not depressed. Pigmentless, excepting pale brownish grey clitellum, in alcohol. Prostomium tanylobous; its anterior half, and ventral surface bisected but body only weakly canaliculate; peristomium short. First dorsal pore 5/6 (P), 6/7 (H). Setae 28 in XII, 47 caudally; *aa* and, mostly, *zz* conspicuous breaks; *a* lines regular, *z* lines irregular, in hindbody and with some irregularity in first few segments; in XII, *aa:ab:bc:cd:yz:zz* = 2.2:1.0:1.2:1.0:1.0:6.6; setae *a* and *b* absent from XVIII. Nephropores clearly visible a short distance behind clitellum near anterior borders of their segments, laterally situated, in straight longitudinal lines in setal lines 11 or near this; not observed (though present) in forebody. Clitellum annular, XIV-XVII but dorsolaterally from anterior 1/3XIII; dorsal pores occluded in 14/15 to 16/17 where these intersegments are weaker. Male pores a pair of minute pores, in *ab*, each with a whitish rim, on large porophores which expand XVIII anteriorly and posteriorly and are somewhat medianly inclined so that male pores seem to be near their median borders; *a* deep depression

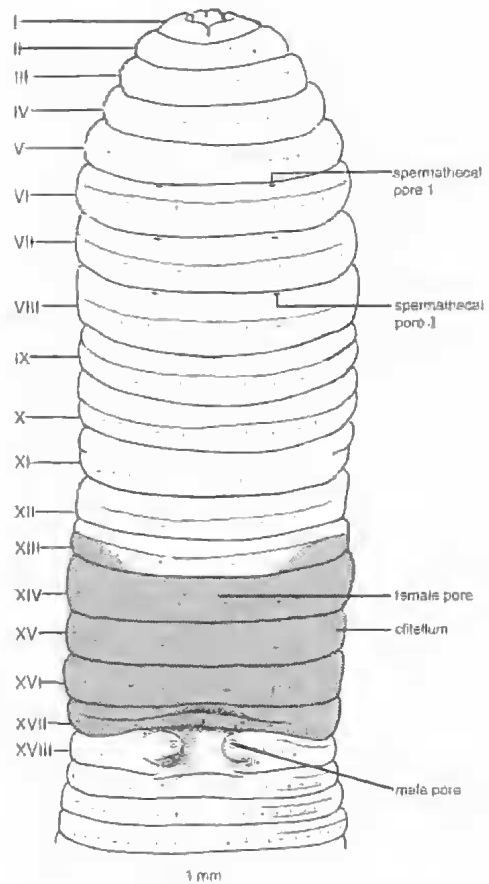


FIG. 3. *Terrisswalkerius covacevichae* sp. nov., holotype, QMG211447. Forebody and clitellar region, ventral view.

present between porophores and behind setal arc of XVII. Accessory genital markings absent (H, P). Female pores small transverse slits immediately anteromedian to setae *a* of XIV (P). Spermathecal pores 3 pairs of simple transverse slits at anterior borders of VI, VII and VIII, in *b* lines, sometimes hidden in anterior intersegmental furrow (H, P).

Thickest septa 10/11-12/13, strongly thickened. Dorsal blood vessel single, continuous onto pharynx. Last hearts in XII; those in X-XII large and arising from supra-oesophageal without recognizable connection to dorsal vessel; those in VII-IX slender, and dorsoventral only. Gizzard large, barrel-shaped with anterior rim, and strongly muscular, in VI; septa 6/7 and 7/8

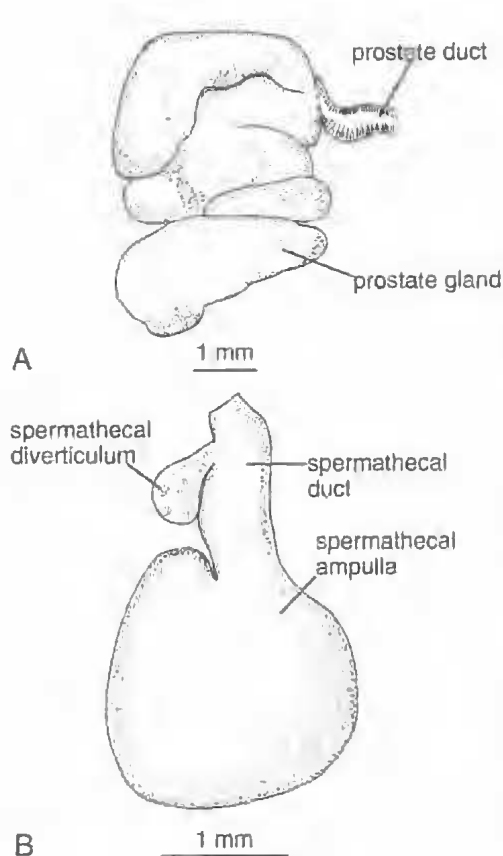


FIG. 4. *Terrisswalkerius covacevichae* sp. nov., holotype, QMG211447. A, Right prostate, ventral view; B, right anterior spermatheca, ventral view.

diaphanous and applied to its posterior surface; gizzard deflecting septa posteriorly so that its posterior end is invested by a pair of long, anteriorly projecting lobes of seminal vesicles of IX. Oesophagus with circumferential vascular striae in IX-XVI, virtually obliterated by gizzard in VII and VIII; greatly expanded in XV and XVI where it attains the width of the intestine; dilatation not constricted off from oesophageal lumen but slightly depressed middorsally, giving a suggestion of a paired condition and internally with circularly arranged, moderate vascular rugae. Oesophagus narrow and whitish in XVII and XVIII. Intestinal origin XIX, although bulging forward so as to appear to commence in XVIII; typhlosole and caeca absent (H, P). Intestinal contents a fine reddish 'silt', of unknown composition, and vegetable matter (including, in H, a recurved thorn filling much of lumen). Nephridia stomate, vesiculate holonephridia; in anterior

region of forebody duct is bent on itself and distal limb is dilated as an elongate bladder which extends at bend as a very short diverticulum; in intestinal region duct joins bladder near its equator and an elongate diverticulum extends laterally from bladder; egress of bladders at body wall is more lateral in intestinal region than further anteriorly (H, P). Holandric; testes (?) and fairly small scarcely iridescent funnels in X and XI; large racemose seminal vesicles with several large loculi which are themselves further subdivided, in IX and XII (H, P); those in IX with a median wing-like or tongue-like portion which extends onto gizzard (H) or this extension not evident, although investing gizzard (P). Ovaies, each a large plate of oocytes, and small funnel, in XIII. Prostates with massive glands enveloping and concealing alimentary canal, in XVIII-XXI; deeply incised by septa but otherwise smooth surfaced and not notably subdivided. Spermathecae 3 pairs, each with a large, ovoid ampulla and a well developed only slightly shorter duct; duct bears, at its ectal fourth, a subspheroidal, almost sessile, inseminated diverticulum. By internal septation there are no spermathecae in VIII, segment anterior to that containing anterior seminal vesicles, last pair of spermathecae being in VII. However, external examination confirms the posterior pair of spermathecal pores anteriorly in VIII. The internal septation is therefore anomalous, disagreeing with external segmentation (H, P).

ETYMOLOGY

Named for Ms Jeanette Covacevich.

REMARKS

Although in the key *T. covacevichae* forms a couplet with *T. canaliculatus*, the latter differs substantially in the following features: α is wider, nephropore rows are irregular, male and spermathecal pores are more lateral, intestinal origin is more anterior (XVII), nephridial bladders are adiverticulate, and seminal vesicles are in XI and XII.

Terrisswalkerius mcdonaldi sp. nov. (Figs 5; 6A,B)

TYPE LOCALITY

17°38'S. 145°32'E., Majors Mtn. N.E. Queensland, coll. J. Covacevich, K.R. McDonald and R. Raven, 14-19.iv. 1978.

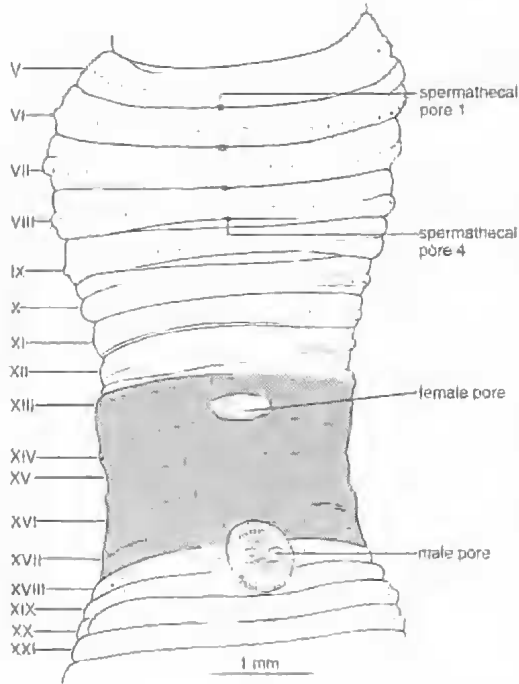


FIG. 5. *Terrisswalkerius mcdonaldi* sp. nov., holotype, QMG211450. Region of male and spermathecal pores, ventral view.

MATERIAL EXAMINED

HOLOTYPE: QMG211450 ex QMGH1994

DESCRIPTION

Length 31mm, width (midclitellar) 2.4mm, segments 106. Body not depressed. A faint trace of purplish pigmentation dorsally in alcohol. Prostomium tanylobous (?); body not canaliculate. First dorsal pore 4/5. Setae 36 in XII; 36 caudally; ventral and dorsal interruptions small but visible throughout in XII $aa:ab:bc:cd:yz:zz = 1.8:1.0:1.0:0.7:1.1:1.8$. Nephropores not externally recognizable. Clitellum annular, yellow brown, 1/2 XIII-XVII; intersegmental furrows obliterated; dorsal pores occluded. Male pores a pair in setal arc of XVIII, on very small papillae separated medianly by a minute papilla, situated in an elongate oval area which extends from setal arc of XVII to posterior XIX and has a tumid rim surrounding a depressed and apparently glandular area anterior and posterior to male papillae. Female pores paired (?) in a transverse slit shortly anterior to setal arc of XIV, in a transversely oval slightly tumid field. Spermathecal pores 4, un-

paired, midventral, in 5/6-8/9, not recognisable unless intersegmental furrows are held open.

Dorsal blood vessel single. Last hearts in XII. Gizzard large, firmly muscular, in VI (?), with conspicuous anterior rim; preceded by a large, but not dilated, soft-walled proventriculus. Oesophagus with a pair of circumferential blood vessels, and dilated, in XIV, XV and XVI, with many discrete internal vascular folds; these dilations not constricted off from oesophageal lumen, but probably to be considered true calciferous glands; oesophagus in XVII short and narrow and invaginated into posterior face of calciferous glands of XVI. Intestinal origin XVIII; typhlosole absent; contents finely particulate vegetable matter. Nephridia stomate, avesiculate holonephridia; each discharging at body wall through a long duct which, although lacking a bladder, has a clearly visible lumen; egress of ducts is in vicinity of setal rows 10 and 11 in forebody and in anterior intestinal region, the row on each side not notably irregular. Holandric; large, iridescent free funnels in X and XI; seminal vesicles small but elongate in XI, very small in XII, not subdivided into loculi. Ovaries, with several delicate strings of oocytes, which are terminally large, in XIII; ovisacs not recognizable. Prostates tubuloracemose, externally thickly tubular and almost smooth walled with some minute surface papillation, restricted to XVIII in which they extend laterally from their ducts; the distal third recurved on remainder of gland; each muscular duct describing a posterolateral loop; conjoined vasa deferentia of its side joining duct at about one seventh of its length from gland. Penial setae absent. Four unpaired spermathecae present, each with a tortuous

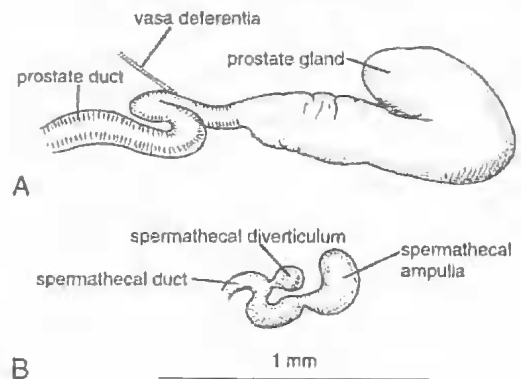


FIG. 6. *Terrisswalkerius mcdonaldi* sp. nov., holotype, QMG211450. A, right prostate; B, right spermatheca of VIII.

digitiform or narrowly saccular ampulla, continuous with and not demarcated from is duct; a subspheroidal diverticulum almost sessile on spermatheca at a point which arbitrarily may be considered the ental end of duct.

ETYMOLOGY

For Keith R. McDonald.

REMARKS

Terrisswalkerrus mcdonaldi appears closest morphologically and, presumably phylogenetically, to *T. (=Diporochaeta) millaamillaa* (Jamieson, 1976b), from nearby Millaa Millaa. *T. millaamillaa* is also a very small species resembling *D. mcdonaldi* in location of the first dorsal pore in 4/5; nephropores in straight or nearly straight rows; clitellum on XIV-XVII; male pores median to *a* lines in an oval field; absence of accessory genital markings (as in all *Terrisswalkerius*); spermathecal pores in 4 intersegments, 5/6-8/9; last hearts in XII; prostates restricted to XVIII, recurved entally, and spermathecae elongate sacciform, with poorly demarcated duct and clavate, almost sessile diverticulum. It differs from *T. millaamillaa* in the unpaired condition of the spermathecal pores which is unknown elsewhere in *Terrisswalkerius* although invariable for *Fletcherodrilus*. Dilatation and internal folding of the oesophagus in *T. millaamillaa* (in XV and XVI) is less developed than in *T. mcdonaldi*.

Terrisswalkerius liber sp. nov. (Figs 7; 8A,B)

TYPE LOCALITY

15°45'S, 145°17'E., Home Rule, near Slaty Ck., N.E. Queensland. Under fallen staghorn fern, Queensland Museum party, 25.x.1974.

MATERIAL EXAMINED

HOLOTYPE: QMG211445 ex QMG9010.
PARATYPE: QMG21446 ex QMG9010.

DESCRIPTION

Length (holotype, H, is posterior amputee) 170 mm (previously dissected paratype, P), width 7 mm, segments 150. Body not depressed. Purplish grey dorsally; intersegmental furrows and ventral surface pale flesh coloured, in alcohol. Prostomium prolobous (H) or very slightly indenting peristomium (P), with open lateral margins extending to half peristomium; deeply canaliculate dorsally and bisected ventrally; body canalicu-

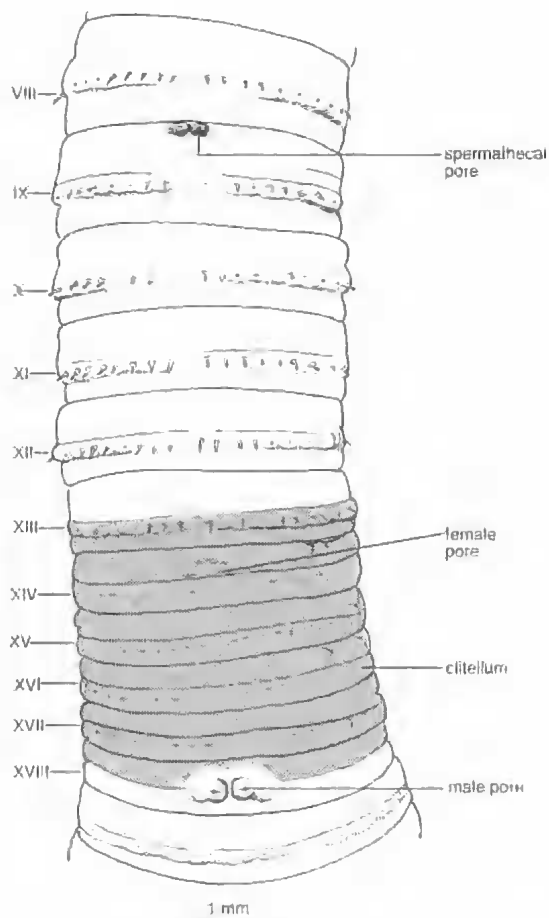


FIG. 7. *Terrisswalkerius liber* sp. nov., holotype, QMG211445. Region of male and spermathecal pores, ventral view.

late. First dorsal pore 5/6 (H, P). Setae 24 in XII; $aa:ab:bc:cd:yz:zz = 2.3:1.0:1.3:1.4:1.9:25.5$; ventral break narrow in forebody but moderately wide in hindbody; dorsal break extremely wide throughout forebody, so that setae are visible only laterally; narrower but very irregular posteriorly; several of the more dorsal rows not visible on clitellum but visible before and behind it; setae in forebody very strongly protruding in a posterior direction. Nephropores, each with a dark encircling field, conspicuous in an almost straight line on each side on clitellum, almost exactly lateral, in setal lines 11 relative to XIII. Clitellum annular, not strongly developed; pale reddish brown; from setal annulus of XIII to presetal annulus of XVIII, inclusive; intersegmental furrows weaker and not paler; dorsal pores retained; canalicula weaker. Male pores cruciform slits, in

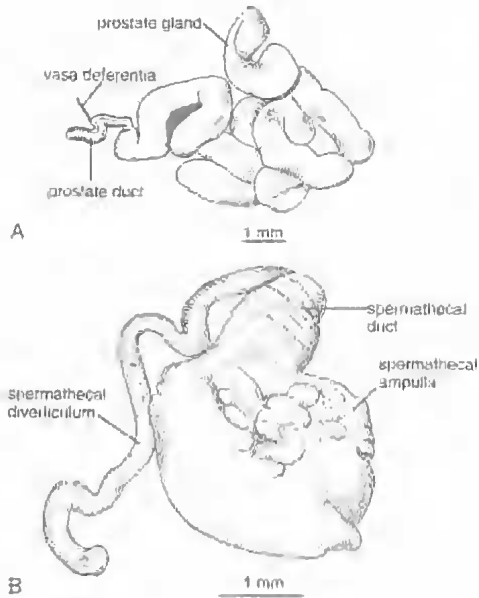


FIG. 8. *Terrisswalkerius liber* sp. nov., paratype, QMG211446. A, right prostate; B, left spermatheca, dorsal view.

setal arc of XVIII, in *a* lines, on a pair of small rounded papillae which are poorly defined laterally and fill middle third of segment and are almost in contact midventrally (H, P). Accessory genital markings absent. Female pores immediately anteromedian to setae *a*, on a low whitish presetal elevation in XIV (H, P). Spermathecal pores 1 pair, shortly posterior to intersegmental furrow 8/9, each a clearly visible minute pore on a very small but well defined wart-like papilla in a common sharply defined depression.

Septa 10/11-12/13 greatly thickened (H). Dorsal blood vessel single; dorsoventral commissurals in V-XII; those in X-XII large, heart-like and latero-oesophageal, originating by a large branch from the supra-oesophageal vessel and a thin, scarcely recognizable branch from the dorsal vessel (H, P). Gizzard very large, elongate and firmly muscular, in V, ensheathed by the extremely thin septa 5/6 and 6/7; its posterior end at level of VIII relative to external segmentation; obliterating oesophagus in VI and VII (H, P); a large muscular proventriculus in IV giving an almost digiceriate appearance (H). Oesophagus segmentally dilated and vascular, with a circumferential blood vessel on each side, in XIII-XVI; but dilatations not cut off from gut. Intestinal

origin 1/2XVII (H, P). Nephridia stomate, vesiculate holonephridia with large pyriform bladders; slender duct joining bladder slightly subterminally in pharyngeal region and increasingly ectal of apex of bladder posteriad but recognition of a diverticulum unwarranted. Holandric; very large iridescent seminal funnels in X and XI; seminal vesicles a pair of large simple almost smooth-surfaced sacs on posterior septum of IX (H, but not P); and anterior septa of XII and, remarkably, XIII (H, P). Ovaries moderate sized laminae of many oocytes ventral to putative seminal vesicles of XIII (H, P). A pair of small sacs on anterior face of XIV may be ovisacs. Prostates slender, tubular and much coiled, in XVIII and XIX (P), or extending into XXI (H); slender muscular sinuous ducts discharging near midventral in XVIII, each receiving parallel vasa deferentia of its side at midlength (H, P). Spermathecae a single pair, each with a very large saccular ampulla with, in its ectal half, a papillated surface, a well demarcated annulated duct; and a terminal, tubular, sinuous, inseminated diverticulum which is longer than combined ampulla and duct (H, P).

ETYMOLOGY

From the Latin *liber* = free, reflecting the name of the type-locality.

REMARKS

Terrisswalkerius liber is very similar morphologically to *T. nashi* (Jamieson, 1976b; see below) and is undoubtedly its sister-taxon. Of the few species of the genus with a single pair of spermathecal pores, *T. liber* and *T. nashi* are the only ones in which they are at intersegment 8/9. *T. liber* differs in the close apposition of the spermathecal and male pores which are significantly wider apart in *T. nashi*. Sympatry of *T. nashi* and *T. liber* at Home Rule strengthens rather than weakens the grounds for separating the two entities and the difference in separation of the genital pores suggests that interbreeding would not occur between the two forms. Nevertheless, reproductive isolation remains to be established.

Terrisswalkerius nashi (Jamieson, 1976b) comb. nov.

Diporochoeta nashi Jamieson, 1976b: 41-42, figs 1, 11b, 14j, 15m, 16n-p, table 2.

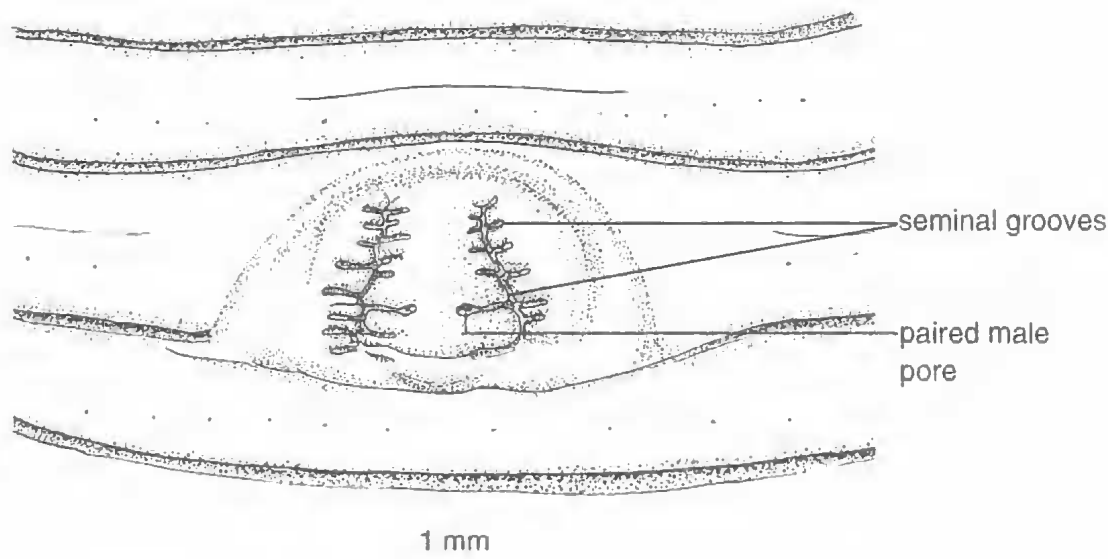


FIG. 9. *Fletcherodrilus menurus* sp. nov., holotype, QMG211435. Lyrate condition of seminal grooves and two putative male pores when male field is extruded.

TYPE LOCALITY

16°34'S.145°17'E., Mt Lewis, rainforest.
16°05'S.145°28'E., Cape Tribulation, rainforest.
15°55'S.145°21'E., Bloomfield River Mission,
S. of Cooktown. All Queensland.

MATERIAL EXAMINED

HOLOTYPE: QMG8357, Mt Lewis.

PARATYPES: QMG8358; 7 specimens, QMG8359-8364; Leiden Museum (LM)15242; 9 specimens, LM15243-15251; LM15252; QMG98373.

NEW RECORDS: QMG8987, 15°46'S. 145°20'E., Mt Hartley, via Home Rule, C. Tanner, J. Covacevich, V. Davies & T. Tebble, 1 specimen; QMG8988, 15°45'S. 145°17'E., Home Rule, under log, near Slaty Ck, granite track, closed forest, K. McDonald, D. Joffe & J. Covacevich, 11. xi. 1974, 1 specimen in two pieces. QMG8989, Home Rule, on track near falls, T. Tebble, 23. x. 1974, 1 specimen; QMG9158, Twelve Mile Scrub, Gap Creek, under rock, V. Davies 28. xi. 1975; QMG9209, 16°34'S. 145°17'E., Mt Lewis, dense moist rainforest with palms, under and in logs, R. Raven, 7 Nov. 1975; QMG10294, 15°42'S. 145°13'E., Helenvale, 12m scrub, in rainforest, P. Filewood, 24.vii.1976.

REMARKS

Specimens with a single pair of spermathecal pores, in intersegmental furrow 8/9 (a feature restricted in *Terrisyswalkerius* to *T. nashi* and *T. liber*), and with these pores and the male pores

well separated, being in the vicinity of setal lines *bc* to *cd* or *d*, represent new records of *T. nashi*. All have the extremely wide dorsal interruption of the setal rings in the forebody, so that almost the entire dorsal surface lacks setae, a condition seen also in *T. liber*. A previously dissected specimen from Twelve Mile Scrub confirms presence of a long tortuous spermathecal diverticulum (the diverticulum of the left spermatheca passing under the ventral nerve cord, in this specimen, as occurs in *Fletcherodrilus*); sperm funnels in X and XI; seminal vesicles in XII and XIII, as also in the new Mt Lewis material (though the additional pair in IX, in the type-description, are not present); last hearts in XII; conspicuous pyriform nephridial bladders; and ovaries in XIII below the putative seminal vesicles. All of these internal features are also seen in *T. liber*. Dorsal mamillations of the spermathecal ampullae, as in *T. liber*, are seen in the specimen from Twelve Mile Scrub but not in that from Mt Lewis.

Fletcherodrilus Michaelsen, 1891 emend.

DIAGNOSIS

Unpaired male and prostatic pores; calciferous glands in XIII-XV; intestinal origin in XVIII; thickly tubular (tubuloracemose?) prostates;

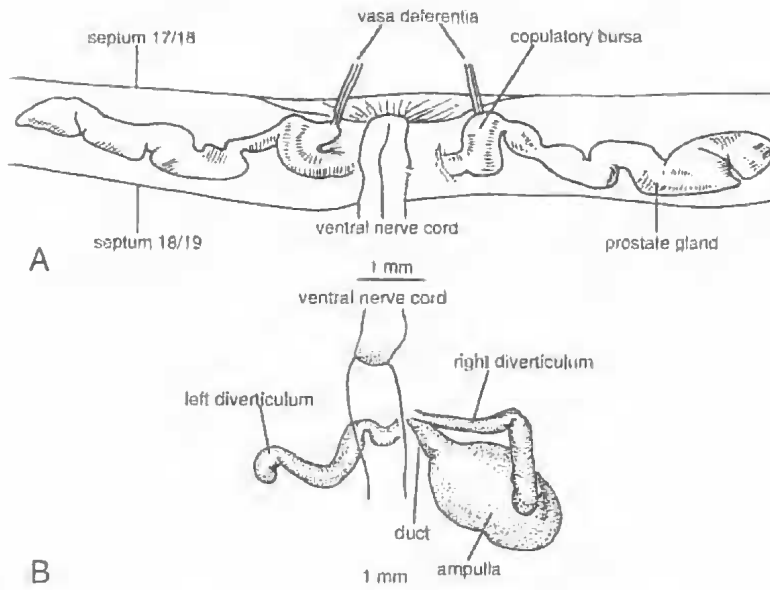


FIG. 10. *Fletcherodrilus menurus* sp. nov., holotype, QMG211435. A, dorsal dissection to show prostate glands; B, spermatheca of IX.

junction of vasa deferentia with the prostate ducts well ectal of the glands; spermathecae with irregularly ovoid ampullae and digitiform diverticula at the body wall.

DESCRIPTION

Medium to large terrestrial worms (85-325mm) with < c. 200 segments. With strong purplish to brown parietal pigmentation. Prostomium slightly epilobous to epitanylobous. Body dorsally canaliculate. First dorsal pore 4/5 or 5/6. Setae 8 to numerous in setigerous segments; if 8, setae c and d distant, not paired. Penial setae absent. Nephropores in d lines or (*sigillatus*) in a sinuous line. Clitellum annular, occupying 4 to 5 1/2 segments, beginning in XIII or XIV. The combined opening of the male and prostatic pore unpaired, midventral. Accessory genital markings present (midventral plications in the vicinity of the spermathecal pores) or absent. Female pores anteromedian to setae a of XIV, inconspicuous. Three or 5 unpaired, midventral spermathecal pores, ending at 8/9.

Some preclitellar septa thickened. Gizzard well developed, in VI or VII. Calciferous glands lateral, sessile pouches in XIII and XIV or XIII, XIV and XV, with internal laminae but not constricted off from the oesophagus. Intestine commencing in XVIII; typhlosole and caeca absent. Dorsal blood vessel continuous onto the pharynx. Last hearts in XII; those in X-XII latero-

oesophageal. Supra-oesophageal vessel in IX (and further forward?) to XII and XIII. Subneural vessel absent. Nephridia stomate, vesiculate holonephridia; postseptal bodies commencing in II; bladders with or without lateral diverticula. Testes and funnels free, in X and XI; seminal vesicles 4 pairs, in IX-XII, or 2 pairs in XI and XII, with or without pseudovesicles in X. Ovaries and funnels in XIII; ovisacs absent. Prostates thickly tubular (tubuloracemose?); vasa deferentia joining the muscular prostate ducts ectal to the glands to as far as the midlength of each duct; the ducts sometimes at least

discharging through a midventral bursa. Spermathecae unpaired, each discharging anteriorly in its segment; duct shorter than the ampulla and bearing ectally 1 or 2 digitiform diverticula.

DISTRIBUTION

Widespread from the Richmond River, New South Wales, to Cape York Peninsula, Queensland.

TYPE SPECIES

Cryptodrilus (?) *unicus* Fletcher, 1889.

INCLUDED SPECIES

F. affinis (Stephenson, 1933); *F. fasciatus* (Fletcher, 1890); *F. menurus* sp. nov.; *F. sigillatus* (Michaelsen, 1916); *F. unicus* (Fletcher, 1889).

KEY TO SPECIES OF *FLETCHERODRILUS*

1. Setae 8 per segment 2
 Setae > 8 per segment 4
2. Spermathecae each with a single diverticulum *F. affinis*
 Spermathecae each with two diverticula 3
3. Body uniformly pigmented though paler ventrally. Gizzard in segment VI. Calciferous glands 3 pairs, in XIII, XIV and XV. Seminal vesicles 2 pairs, in X and XI *F. unicus*
 Body with transverse pigmented stripes. Gizzard in segment VII. Calciferous glands 2 pairs, in

TABLE 1. *Fletcherodrilus menurus*. Setal ratios in segment XII.

	aa	ab	bc	cd	yz	zz
Holotype	1.4	1.0	1.3	1.0	1.2	2.5
Paratype 1	1.3	1.0	1.0	0.9	1.6	4.7
mean of 2	1.35	1.0	1.15	0.95	1.4	3.6

XIII and XIV. Seminal vesicles 4 pairs, in IX-XII *F. fasciatus*

4. Spermathecal pores 3, midventrally, in 6/7, 7/8 and 8/9. Ventral surface in VII-IX tumid and with several longitudinal (glandular?) plications *F. sigillatus*

Spermathecal pores 5, midventrally in 4/5 to 8/9. An oval, superficially pleated genital marking midventrally in VIII *F. menurus* sp. nov.

***Fletcherodrilus menurus* sp. nov.**
(Figs 9; 10A, B; 11; 12)

TYPE LOCALITY

18°56'S, 146°13'E., Mt Spec National Park, North Queensland, under logs and rocks in rainforest, K.R. McDonald, R.A. Atherton, 4.i.1977.

MATERIAL EXAMINED

HOLOTYPE: QMG211435.

PARATYPES: QMG211436-211441.

DESCRIPTION

Length 140-199mm, width (midclitellar) 6 mm, segments 202 (P6), 204 (P1). Form dorsoventrally slightly depressed. Pigmented purplish brown dorsally, buff ventrally. Prostomium epilobous 1/3- >1/2, closed, but with lateral margins continuing to 1/2 or 2/3 peristomium (sometimes flanked by other longitudinal furrows); it and entire body with a narrow mid-dorsal longitudinal groove (canalicula); prostomium also bisected ventrally (H, P1-6). First dorsal pore 5/6 (H, P1-6). Setae 40 (H), 36 (P1) in XII; 41 (H), 36 (P1) in XX; caudally, about 12 segments from posterior end, 44 (H, posterior amputee), 29 (P1); ventral gap not apparent in forebody, becoming recognisable on clitellum, not apparent far caudally; dorsal gap conspicuous but not large, and only slightly irregular, throughout. Setal ratios (Table 1).

Nephropores sporadically visible; in setal lines 14 in XIV; setal lines 7 in XVIII. Clitellum annular, greyish brown; 1/2XIII-XVIII, but interrupted ventrally in XIII, sometimes weakly developed dorsally to 1/2XIX; intersegmental furrows retained but not as sharp as elsewhere;

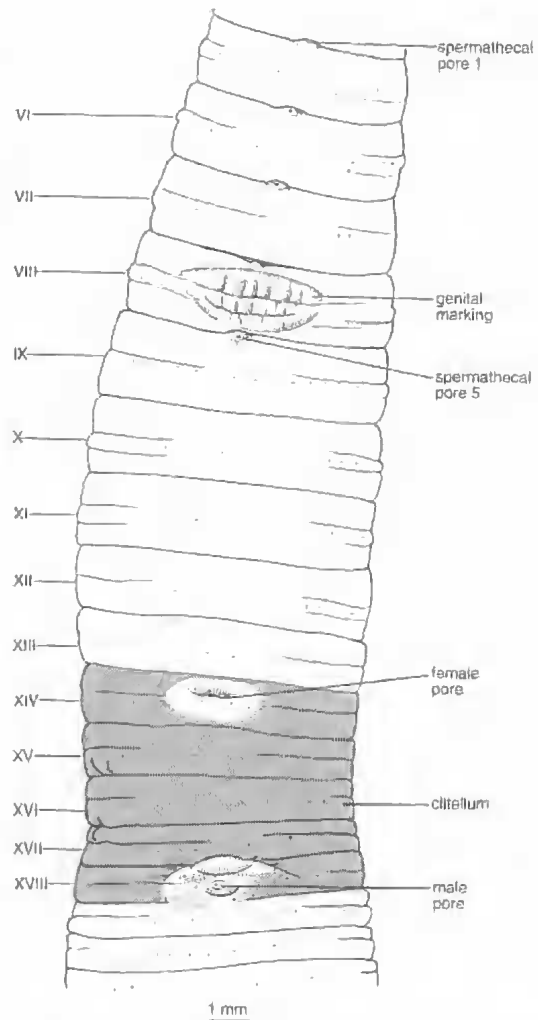


FIG. 11. *Fletcherodrilus menurus* sp. nov., paratype, QMG211436. Region of male and spermathecal pores, ventral view. Showing single male pore when male field is withdrawn.

dorsal pores occluded (H, P1). The male genital field shows two distinct forms which are here deduced from dissection to be stages in eversion. In the holotype, what may be termed the 'lyrate' condition obtains. Here the two minute male pores, posterior to the setal arc of XVIII and well median of setal lines *a*, being 0.4mm apart; each is connected by a short laterally running groove to a longitudinal groove which itself gives off short side branches. The longitudinal grooves are slightly convergent anteriorly. The male pores and the system of grooves lie in an approximately circular depressed field which extends almost to the anterior border of XVIII, where it is bordered

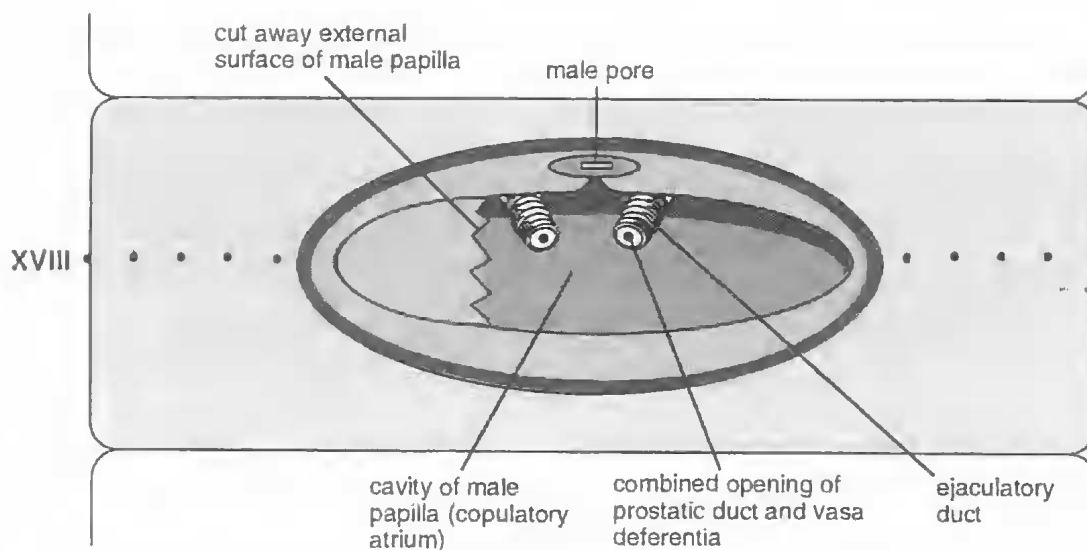


FIG. 12. *Fletcherodrilus menurus* sp. nov., paratype, QMG211441. Semidiagrammatic representation of dissection of male porophore by transverse incision, revealing internal bursa with two male pores.

by a semicircular rim, and extends onto the anterior region of XIX. In the other paratypes, in marked contrast, the male pore appears unpaired, midventral in the setal arc of XVIII, as a minute slit in a very small low, oval papilla. Transverse incision of the male papilla in paratype 6 (QMG 211441) reveals an inner cavity or bursa (Fig. 12) from the rear (dorsal) wall of which projects a pair of muscular ducts, the ectal end of the prostatic ducts. It is therefore deduced that the lyrate condition is brought about by eversion of the dorsal wall of the bursa and that when this is retracted it leaves a single pore at the surface of the papilla. Accessory genital marking a large transversely oval pad midventrally in VIII, extending laterally to about setal lines 5, traversed by a deep furrow which coincides with the anterior margin of the setal annulus; longitudinal pleats arising from this furrow (P1 and paratypes 4-6; not present in holotype). Female pores paired, minute, immediately anteromedian to setae *a*, concealed in a transverse furrow which has tumid margins. Spermathecal pores 5, unpaired, midventral, in intersegmental furrows 4/5-8/9, each on a small, low oval papillae which creates a semicircular forward indentation of the furrow.

Last hearts in XII; those in X-XII latero-oesophageal. Supra-oesophageal vessel in X-XVI (H, P1). A subneural vessel present (P1). Gizzard large, elongate, and moderately firm, in

VI, deflecting the diaphanous septum 6/7 posteriorly; septum 5/6 very delicate and attached shortly anterior to middle of gizzard (H) or near its anterior rim (P1), giving the impression that this septum primitively passed to rear of gizzard; a wide, flaccid proventriculus present in segment IV. Oesophagus with circumferential vascular striae in IX-XVI, especially XII-XVI; in each of XIII, XIV and XV dilated on each side of dorsal vessel, and with moderately high radial laminae on its lateral walls; these dilations not constricted off from oesophageal lumen, but to be considered true calciferous glands. Intestinal origin in XVIII but in P1 not widening until XIX; typhlosole absent. Gut contents include large pieces of sclerophyllous leaves or vegetable fibres and quartz grains. Nephridia stomate, vesiculate holonephridia; bladders very large, elongate-fusiform wide, adiverticulate tubes, joined at ental extreme by nephridial duct, each ectally continued to pore as a long narrow duct; egress of ducts is near dorsal in II, slightly more ventral in III, and thereafter progressively more ventral until in anterior intestinal region it forms an irregular, ventrolateral or ventral line (H) or still far dorsal, though in slightly irregular longitudinal rows (P1). Holandric; small free funnels in X and XI; seminal vesicles on anterior septa of XI and XII, not subdivided into loculi (H) or also (pseudovesicles?) X, each with a few large loculi

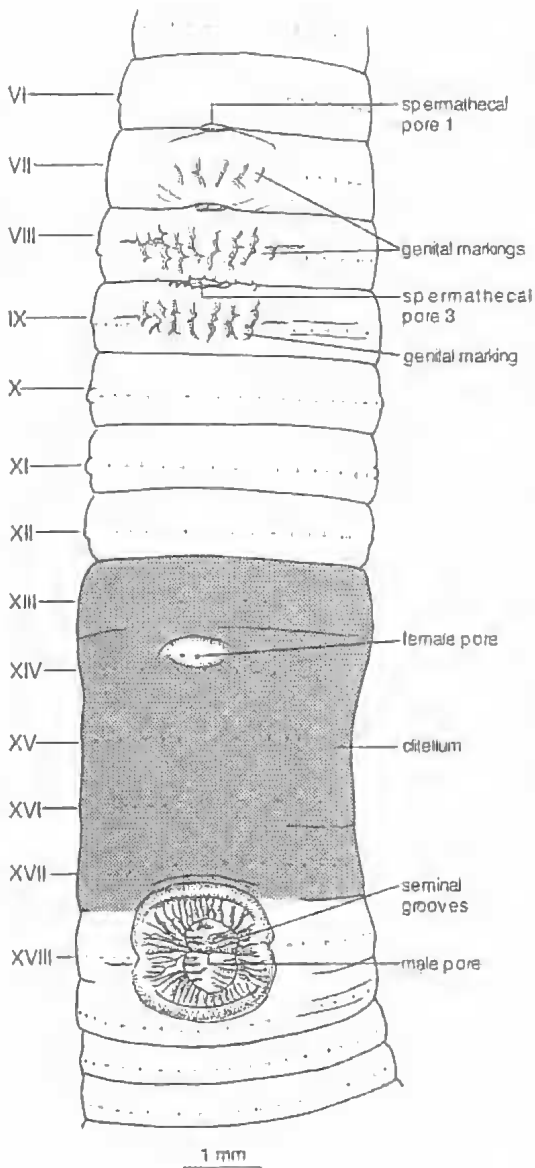


FIG. 13. *Fletcherodrilus sigillatus* (Michaelsen, 1916). Wallacha Falls. Region of male and spermathecal pores, ventral view.

(P1). Ovaries small masses with few large terminal oocytes in XIII (H), not developed in P1; ovisacs not recognisable. Prostates tubuloracemose, externally thickly tubular and smooth walled, restricted to XVIII in which they wind laterally from their ducts (H); right prostate compacted as a single large lobe with no subdivision (P1); each muscular duct widens in its

ectal half to form a bursa which is fused along most of its length to body wall; conjoined vasa deferentia of its side joining anteromedian limit of bursa (H, P1). Penial setae absent. Five unpaired spermathecae present, increasing size posteriad, each with large, irregularly ovoid ampulla, tapering duct and 2 tubular, tortuous, inseminated diverticula which enter body wall on either side of duct; ampullae lying to one or other side of ventral nerve cord and contralateral diverticulum passing under the cord; first three ampullae are on left and last two on right of the cord (H) or those of V and VIII, only, are on the left (P1).

ETYMOLOGY

From *Menura*, the lyre-bird, referring to the similarity of the configuration of the seminal grooves to the tail of this bird.

REMARKS

Fletcherodrilus menurus is clearly the sister-species of *F. sigillatus*. Both show a striking departure from the other species of *Fletcherodrilus*, *F. unicus* (Fletcher, 1889), *F. affinis* (Stephenson, 1933) and *F. fasciatus* (Fletcher, 1890), in the development of accessory genital markings and in the perichaetine condition of the setae. The genital markings consists of longitudinally pleated areas and are of a type unknown elsewhere. Development of these markings represents a remarkable apomorphic departure from the absence of markings throughout the remainder of the monophyletic *Fletcherodrilus-Terrisswalkerius* clade. *F. menurus* is well defined from, and presumably plesiomorphic relative to, *F. sigillatus* in having 5 spermathecal pores in contrast with the 3 pores in the latter. Furthermore, the 'lyrate' condition of the putative seminal grooves of the male field in *F. menurus* differs from the anteroposteriorly duplicated, mirror image, array of grooves in *F. sigillatus*.

Dissection of the male porophore of a specimen with a single male pore, revealing two internal prostate pores (Fig. 12) is here considered to indicate that such specimens are conspecific with the externally lyrate holotype with its two male orifices. In the unlikely event of this being shown not to be the case, the name *F. menurus*, would be restricted to lyrate individuals.

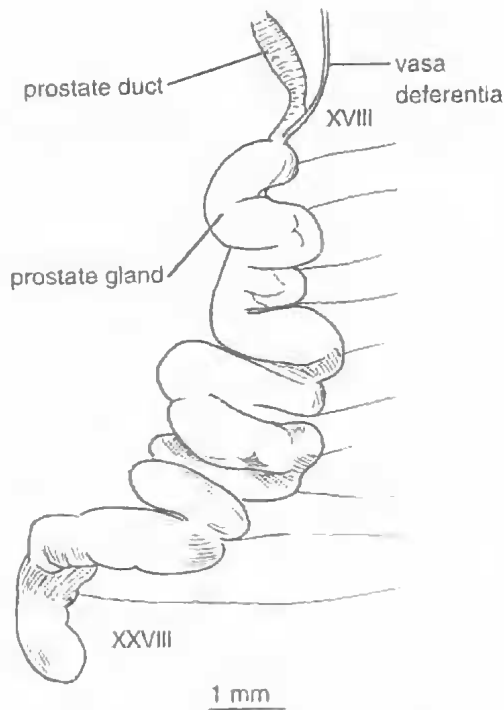


FIG. 14. *Fletcherodrilus sigillatus* (Michaelsen, 1916). Wallacha Falls. Right prostate.

Fletcherodrilus sigillatus (Michaelsen, 1916)
(Figs 13; 14; 15)

Perionyx (*Diporochoeta*) *sigillatus* Michaelsen, 1916:
16-19, pl. 1, figs 3, 4.

Diporochoeta sigillata; Jamieson, 1971c: 83.

Fletcherodrilus ? *sigillatus*; Jamieson, 1974a: 221.

Fletcherodrilus sigillatus; Jamieson, 1976b: 9.

TYPE LOCALITY

17°21'S. 145°36'E., Malanda, in Cairns District, Qld.

MATERIAL EXAMINED

SYNTYPES: Royal Stockholm Museum, NHRS 1951. Zoology Museum, Hamburg, HMV8475.

OTHER RECORDS: 17°13'S. 145°50'E., Wallacha Falls, Palmerston National Park, T. Walker, 1 specimen (Jamieson collection); 17°38'S. 145°32'E., Majors Mtn. N.E. Queensland, J. Covacevich, K. McDonald. R. Raven, QMGH1994 (ex QMGH1968); 17°17'S. 145°37'E., Lake Eacham, closed forest, under sheet of corrugated iron, K. McDonald, J.D., 21.ix. 1974, QMG9000; 18°04'S. 144°52'E., 40 Mile Scrub, c. 62 km W Mt Garnet, under logs, R. Raven, QMGH1976; 17°23'S. 145°39'E., Pelling's fragment

of rainforest, South of Tarzali, near Atherton, Craig Moritz, 18 Aug 1994, QM211455. All in Queensland.

DESCRIPTION

Length 101-170mm, width (midclitellar) 4.5mm, segments 148-(180?). Form dorsoventrally slightly depressed. Pigmented purplish brown to dark flesh coloured dorsally, pale, greyish ventrally. Prostomium epitanalybous, it and entire body with a narrow middorsal longitudinal groove (canalicula). First dorsal pore 5/6 but an imperforate rudiment at 4/5. Setae 34/XII; 32/XX; caudally 38 (33/IX, 34/XII, XXII, 36/XXVI, Michaelsen); rows slightly more widely spaced ventrally than dorsally; ventral gap (*aa*) recognisable only behind clitellum, maximally (posteriorly) 2 *ab*; dorsal gap (*zz*) visible throughout, anteriorly = 2 *zy*; posteriorly = 4 *zy* but narrowing posteriad as setae are more closely spaced caudally. Nephropores: a pair in each segment, commencing anteriorly in II, but forming an irregular sinuous line on each side, varying in position from near middorsum (in II) to dorsolateral, lateral, or ventrolateral and only occasionally symmetrically disposed in a segment. Clitellum annular, XIII, 1/2 XIII-1/2XVII, XVII. Male pore unpaired, midventral equatorially in XVIII at bottom of a deep pit of specialized epithelium which extends anteriorly and posteriorly almost to setal arcs of XVII and XIX and laterally to setal lines 4-6, margin of pit slightly thickened and a little indented at setal arc of XVIII; bottom of pit in vicinity of male pore differentiated as an elliptical field, around pore, traversed by a conspicuous equatorial furrow in which male pore lies, this central field pleated by several, mostly transverse ridges; walls of pit with similar plications extending radially from central field. Discrete accessory genital markings absent but ventral surface in VII-IX tumid and with several longitudinal (glandular?) plications. Female pores paired, close together, shortly anteromedian of (or, Michaelsen, in front of) setae *a* of XIV. Spermathecal pores 3, unpaired, midventral, in 6/7, 7/8 and 8/9, each an eye-shaped aperture with tumid, almost papillate margins.

Last hearts in XII; those in X-XII latero-oesophageal. Supra-oesophageal vessel in IX-XIII; moderately developed. Gizzard large and moderately firm, in VI; septum 5/6 very delicate and attached near anterior limit of gizzard, giving the impression that this septum primitively passed to rear of gizzard; a wide, flaccid proventriculus present in the segment preceding

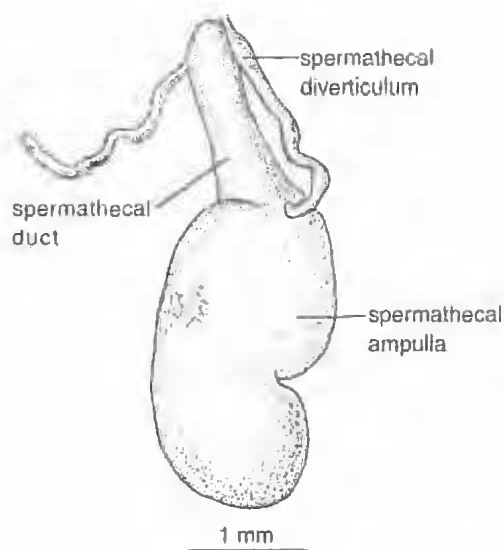


FIG. 15. *Fletcherodrilus sigillatus* (Michaelsen, 1916), Wallacha Falls. Spermatheca of IX.

gizzard. Oesophagus with circumferential vascular striae in IX–XVI; in each of XIII, XIV and XV dilated on each side of dorsal vessel, and with moderately high vertical laminae on its lateral walls; these dilatations not constricted off from oesophageal lumen, but probably to be considered true calciferous glands. Intestinal origin XVIII; typhlosole absent. Nephridia stomate, vesiculate holonephridia (funnels demonstrated for those discharging in II); bladders very large, elongate-fusiform wide, adiverticulate tubes, joined at ental extreme by nephridial duct, each ectally continued to pore as a long narrow duct which equals bladder in length only when pore is far dorsally. Holandric; funnels slightly iridescent in X and XI; gymnorchous; seminal vesicles racemose in XI and XII. Ovaries (webs of many oocytes) in XIII; rudimentary ovisacs in XIV. Prostates tubuloracemose, externally thickly tubular (c. 1.8 mm long and 0.7 mm wide, Michaelsen) and smooth walled, winding from XVIII to XXVII, each with a central lumen occupying a small fraction of total diameter (one eighth in middle of organ and with many lateral canals, Michaelsen); short but considerable muscular duct joined near glandular portion by vasa deferentia which then run distally in duct wall; transverse muscles present on body wall in vicinity of duct. Penial setae absent. Three unpaired spermathecae present, each with large,

flattened irregularly ovoid ampulla, well demarcated though stout duct and 2 tubular, tortuous diverticula which enter body wall on either side of duct; length spermathecae = 4 mm; ratio length: length duct = 2.7; ratio length: length diverticulum = 1.8.

REMARKS

All that remains of the single type-specimen in the Hamburg Museum, HM(V8475), is an isolated gizzard. Michaelsen reported that the type was strongly macerated and that he was unable to determine with certainty whether the anterior rudimentary seminal vesicles were in X or XI. He concluded that they were in XI but on this basis the gizzard appeared to be in VII, at which he expressed doubt. Calciferous glands were reported for XIV and XV, with a rudimentary pair, hardly to be considered glands, in XVI, and last hearts were stated to be in XIII. This sequence is one segment behind that of the new material dissected, from Wallacha Falls and 40 Mile Scrub, and Michaelsen's fear that it might be incorrect by one segment clearly was warranted.

Despite its perichaetine setal arrangement, Jamieson (1974a: 221) considered this species to be related to *Fletcherodrilus* rather than to *Perionychella* (i.e. *Diporochoeta*). Among its similarities with the three species already placed in *Fletcherodrilus* was the unpaired male and prostatic pores (a condition unknown in *Perionychella* but now known in *Terrisswalkerius mcdonaldii*), presence of calciferous glands in XIII–XV; intestinal origin in XVIII; the thickly tubular prostates; junction of the vasa deferentia with the prostate ducts well ectal of the glands; and the form of the spermathecae with their irregularly ovoid ampullae and digitiform diverticula at the body wall. The presence of diverticula on the nephridial bladders in the other species of *Fletcherodrilus* and their lumbricin setae cannot be considered significant obstacles to inclusion of *F. sigillatus* as these variations occur within *Diporochoeta*. The perichaetine condition is foreshadowed in *F. unicus* in which the posterior setal lines are sometimes irregular and there are occasionally supernumerary setae and a strongly perichaetine condition is now known for *F. menurus*.

Hiatidrilus gen. nov.

DIAGNOSIS

Setae 8 per segment. Male pores in XVIII. Genital markings present. Spermathecal pores 2

pairs, the last at anterior limit of IX. Gizzard large, in V. Oesophageal vascularization, with or without development of extramural calciferous glands, in the vicinity of the hearts. Intestine commencing in XV or XVI. Nephridia stomate holonephridia, with or without bladder-like ducts. Holandric or metandric. Ovaries in XIII. Prostates coiled tubular (or tubuloracemose?). Penial setae present. Spermathecae each with 2 clavate diverticula.

DESCRIPTION

Setae 8 per segment, Dorsal pores present. Clitellum annular or saddle-shaped, in the vicinity of XIII-XVII. Male pores in XVIII, median or lateral off *b* lines. Segmental and intersegmental genital markings present. Spermathecal pores 2 pairs, in or immediately behind 7/8 and 8/9 in *b* lines. Female pores anteromedian or anterior to setae *a* of XIV. Last hearts in XII. Gizzard large, in V. True extramural, pyriform, dorsolateral calciferous glands two pairs, in XI and XII; or oesophagus segmentally dilated and vascular, with large internal villi in IX-XIII but lacking calciferous glands. Intestine commencing in XV or XVI. Nephridia stomate, avesciculate holonephridia; ducts discharging in *c* to *cd* lines, slender or wide and bladder-like. Testes in X and XI or XI only. Ovaries and funnels in XIII; ovisacs absent; pseudovesicles absent or present in XIV. Prostates tubular, much wound, in XVIII and XIX. Penial setae present. Spermathecae each with 2 clavate diverticula.

DISTRIBUTION

Bunya Mountain (South-east Queensland) and Grafton, on the Clarence River (New South Wales).

TYPE SPECIES

Diporochoeta bunya Jamieson, 1976b.

SPECIES INCLUDED

Diporochoeta bunya Jamieson, 1976b; *Cryptodrilus semicinctus* Fletcher, 1890

KEY TO SPECIES OF HIATIDRILUS

- Holandric, with two pairs of male funnels. Genital markings a midventral transverse glandular pad occupying the region in front of the male pores, extending longitudinally from 1/2XVII-1/2XVIII and laterally to include setae *b* of XVII, bearing on each side, a circular whitish genital marking in *b* posteriorly in XVII, and a further one median to setal lines *a* at the site of

the obliterated intersegment 17/18; a further similar pair of circular genital markings present at the anterior border of XIX behind the latter pair, median of *a* lines, each of this pair on an elliptical tumescence extending longitudinally from 1/2XVIII to include setae *ab* of XIX, furrow 18/19 persistent and separating off its anterior region; each ellipse conjoined with that of the other side to form a transverse pad narrowed in the midline. A transversely elliptical tumid pad present midventrally in each of XI and XII filling the segment and including setae *a*, each pad with a pair of circular genital markings median to *a*, the marking on the right in XII may be transversely duplicated *H. bunya*

Metandric, with male funnels in XI only. Genital markings at fullest development small circular boss-like prominences, each surrounded by an elliptical glandular field, unpaired and midventral in 13/14; paired between setae *a* in 14/15, 15/16, and 16/17, those in 14/15 almost contiguous medianly, those in the next two intersegments further apart so that those of 16/17 are shortly median of setae *a*; a small marking on each side in front of and behind the male porophore, lateral of *b* lines, at the posterior and anterior limits of XVII and XIX respectively; paired markings almost contiguous medianly in 19/20 accompanied by a marking in *ab* (the left one bearing a boss); and an unpaired median marking in 20/21. Further genital markings present in the vicinity of the spermathecal pores in or lateral of the lines of ventral setal couples: post-setal in VII and VIII, pre-setal in IX and X, those on the right side transversely duplicated in VII and triplicate in VIII; an additional equatorial marking present on this side in VIII. Additionally the posterior genital field (XIII posteriorly) may be similar though several markings are at least unilaterally absent. Constant are the paired markings at 14/15, 15/16, 16/17, posterior XVII and anterior XIX. The anterior genital markings may be absent *H. semicinctus*

ETYMOLOGY

Hiatidrilus, meaning 'gap worm', referring to its intermediate location between southern *Diporochoeta*s and *Terrisswalkerius*.

REMARKS

The name *Hiatidrilus* refers to the fact that the two known species of this genus, previously referable to *Diporochoeta*, lie in the southern region of the very large geographical hiatus which separates *Diporochoeta*, in Victoria and Tasmania, from the North Queensland species of *Diporochoeta* which have here been transferred to *Terrisswalkerius*.

Presence of two spermathecal diverticula, on opposite sides of the duct, separates this genus from all species of *Diporochoeta* s. lat., excepting the Tasmanian *D. scolecoidea*. The latter species differs significantly in being strongly perichaetine and in having racemose prostates. A supernumerary diverticulum in series with the usual diverticulum occasionally occurs in *D. hobartensis* (Tasmania), and the diverticulum is doubled in *D. willsiensis* (Victoria) but although these two species also have basically eight setae per segment, they have five pairs of spermathecae. A highly distinctive feature of *Hiatidrilus bunya* relative to most *Diporochoeta* species is the possession of true extramural calciferous glands, in XI and XII, although extramural glands occur in the type species, *D. intermedia*, in X and XI. *H. semicinctus* is distinguished in being metandric and having a saddle-shaped clitellum. A detailed account of the distinctive genital markings is given in the key in the absence of specific descriptions.

The two species here referred to *Hiatidrilus* could be placed in separate genera but their differences can reasonably be accommodated in a single genus. The phylogenetic analysis supports their congeneric status. The Bunya Mountains location of *H. bunya* is near the source of the Clarence River by which *H. semicinctus* occurs, giving some geographical validity to recognition of a special relationship between the two species.

Hiatidrilus bunya
(Jamieson, 1976b) comb.nov.

Diporochoeta bunya Jamieson, 1976b, 18-20, figs 1, 11a, 13e, 15e, table 1

TYPE LOCALITY

26°57'S.151°35'E., Bunya Mts., near Festoon Falls-Qld.

MATERIAL EXAMINED

HOLOTYPE: QMG8336.

REMARKS

H. bunya is distinguished from *H. semicinctus* in the key.

Hiatidrilus semicinctus
(Fletcher, 1890) comb.nov.

Cryptodrilus semicinctus Fletcher, 1890: 996-997.

Megascolides semicinctus Beddard, 1895: 494.

Plutellus semicinctus: Michaelsen, 1900: 170; Jamieson, 1971c: 88.

TYPE LOCALITY

29°41'S.152°56'E., Grafton, Clarence River-NSW.

MATERIAL EXAMINED

SYNTYPES: AMW1312 (3 specimens; a fourth is in fact a *Heteroporodrilus*).

REMARKS

H. semicinctus is distinguished from *H. bunya* in the key.

CLADISTIC ANALYSIS

MATERIALS AND METHODS

Twenty nine external and internal characters, representing most features used in megascolecid taxonomy, were listed in a data matrix for 39 species of the tribe Perionychini. These included the type species of all Australian perionychins and the New Zealand type-species of *Diporochoeta*, *D. intermedia*.

Species selected and sources of data were as follows (asterisked species are the type-species of their respective genera):

Diporochoeta capensis: (Jamieson; 1974a); **Diporochoeta intermedia*: Jamieson, 1976a; *Diporochoeta kershawi*: (Jamieson; 1974a); *Diporochoeta mortoni* (Jamieson, 1974a); *Diporochoeta victoricae* (Spencer, 1892a, Jamieson, unpubl.); *Fletcherodrilus menurus* sp. nov.; *Fletcherodrilus stgillatus*: this account, **Fletcherodrilus unicus*: Jamieson & Wampler, 1979; **Graliophilus georgei* Jamieson, 1971b; *Heteroporodrilus* sp.; **Heteroporodrilus tryoni* Jamieson, 1970a; **Hiatidrilus* (= *Diporochoeta*) *bunya* (Jamieson, 1976b); *Hiatidrilus* (= *Diporochoeta*) *semicinctus* (Fletcher, 1890; Jamieson, unpublished); **Paraplutellus insularis* Jamieson, 1972a; **Perionychiella dendyi* (Spencer, 1892b); **Pinguidrilus tasmanianus* Jamieson, 1974a; **Plutellus heteroporus*: Jamieson, 1971d; **Pseudoperichaeta smithi*: Jamieson, 1970a; **Simsia tuberculata*: Jamieson, 1972a, b; **Woodwardiella callichaeta*: Jamieson, 1970a; and the following *Diporochoeta* species here transferred to *Terriwalkeri*: *D. atavicus*: Jamieson, 1976b, unpubl.); *D. athertonensis*: Jamieson, 1976b, and this account; *D. barrouensis*: Jamieson, 1976b; *D. blounti* Jamieson, 1976b; **D. caudiculatus*:

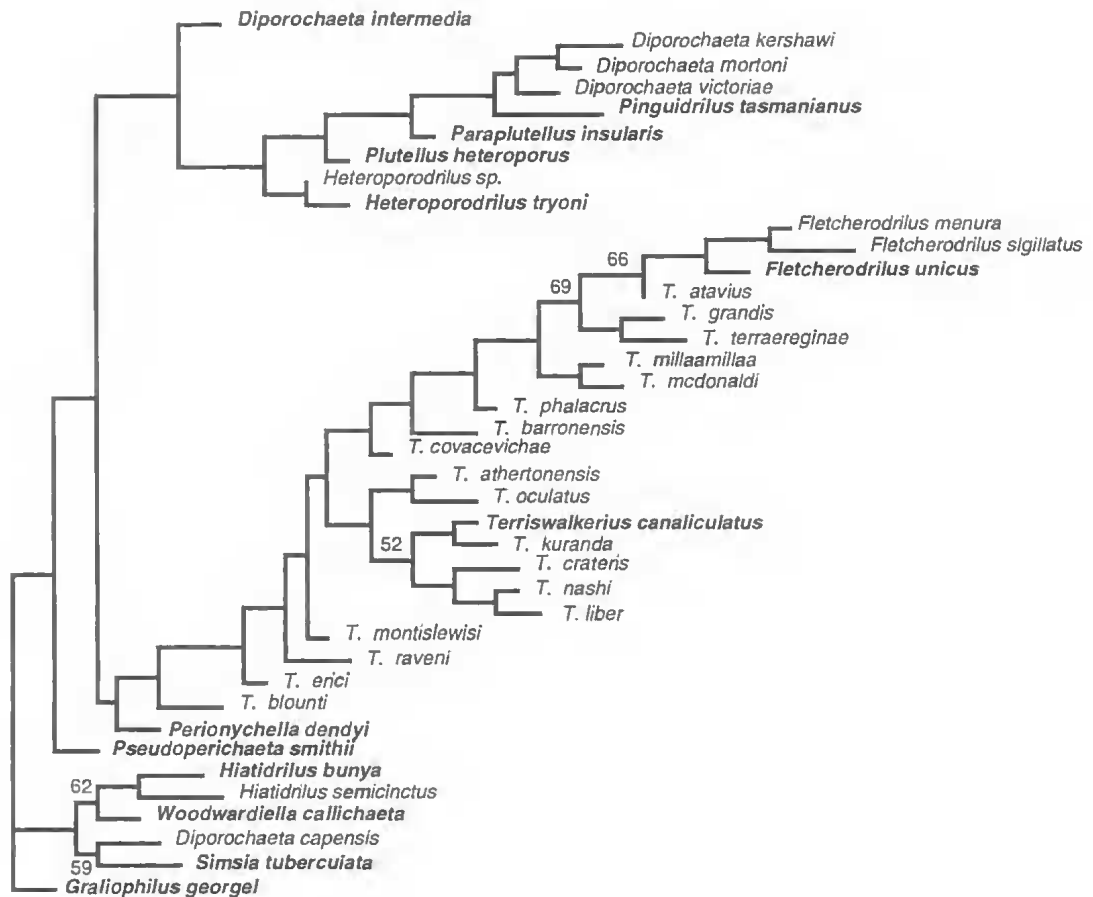


FIG. 16. 50% majority rule consensus tree of 29 equally and most parsimonious trees for the genera of Perionychini, including all known species of *Terriswalkerius*, resulting from an heuristic search (see text).

Jamieson, 1976b; *D. crateris* Jamieson, 1976b; *D. erici*: Jamieson, 1976b; *D. grandis*: Jamieson, 1976b; *D. kuranda*: Jamieson, 1976b; *D. millaamillaa* Jamieson, 1976b; *D. montislewisi* Jamieson, 1976b; *D. nashi* Jamieson, 1976b, and this account; *D. oculata* Jamieson, 1976b; *D. phalacrus* (Michaelsen, 1916; and Jamieson, unpubl.); *D. raveni* Jamieson, 1976b; *D. terraereginae*: Jamieson, 1974b; *Terriswalkerius covacevichae* sp. nov.; *Terriswalkerius liber* sp. nov.; *Terriswalkerius mcdonaldi* sp. nov.

The characters used were as follows:

[1]Body canaliculate: (0) no, (1) yes,

[2]First dorsal pore, at anterior limit of segment: (0) absent, (1) 4, (2) 5, (3) 6, (4) 7, (5) 8, (6) 9, (7) 10, (8) 11, (9) further posteriad,

[3]Setal arrangement: (0) lumbricin, (1) perichaetine,

[4]Nephropore rows: (0) regular, (1) irregular, (2) with complex alternation,

[5]Clitellum, first full segment: (0) 12, (1) 13, (2) 14, (3) 15,

[6]Male pores: (0) single, (1) paired,

[7]Male pores, setal location: (0) median to *a*, (1) *a*, (2) *ab*, (3) *b*, (4) *bc*, (5) *c*, (6) *cd*, (7) *d*, (8) dorsal of *d*,

[8]Female pores: (0) single, (1) paired, (1, Invariable)

Fig. 17. Input Data Matrix

Node	111111111222222222	12345678901234567890123456789
D. intermedia	00102181104101112111510101000	
H. bunya	04002121102302112131502101110	
F. menurus	13112001105012132220810121001	
F. sigillatus	13111001103217112220810171100	
D. kershaw	0200111110500111212070?100110	
F. unicus	12002001005012112230811121001	
G. georgei	0200112110230111313090?101000	
D. capensis	?31?213110230113211060?101010	
P. heteroporus	0402113?10510111?131510100100	
H. sp.	0302213110320111313151010100?	
H. tryoni	0302?21103202313131510101000	
Paraplutellus in.	04022131105001112301611100010	
Pinguidrillus tas.	08012121105000?3130910100010	
Pseudoperichaeta s.	0101212110410111?13090?102000	
S. tuberculata	0100212111230121213080?100010	
W. callichaeta	290021211023011?2120?02102010	
P. mortoni	22001121105001112130811103110	
D. victoriae	14002121105001112130711100100	
H. semicinctus	09002141102302112130600230110	
T. atavilus	?211?10?0500??222??1?20????	
T. athertonensis	13101101003201112130610101000	
T. barronensis	12102161003001132230811120000	
T. blounti	02101131001301112120700101100	
T. canaliculatus	13112171003201112230710181000	
T. crateris	011?2151001201132220710171100	
T. erici	12101111004101112130811101?00	
T. grandis	12112121005001112131700101000	
T. kuranda	1311215100410111?2230710161100	
T. millaamillaa	12102101004101112230800180000	
T. montislewisi	12102131003001112230711101100	
T. nashi	131011510014011132230710190100	
T. oculatus	12101141003202412220710101000	
T. phalacrus	131?2111005001212230900121000	
T. raveni	12102161003001112120711110100	
T. terraereginae	1211211100400111313090?161000	
T. mcdonaldi	0210210100411111223080?121000	
T. covacevichae	1310212?003101112230911101100	
T. liber	1310211?001401132130710170100	
P. dendyl	01102131104101112130900142100	

- [9]Accessory genital markings: (0) absent, (1) present,
 - [10]Spermathecal pores location: (0) intersegmental, (1) significantly segmental,
 - [11]Spermathecal pores, number of segments: (1) 1, (2) 2, (3) 3, (4) 4, (5) 5,
 - [12]Spermatheca first: (0) 5, (1) 6, (2) 7, (3) 8, (4) 9,
 - [13]Spermathecal pores, pairing: (0) paired, (1) single,
 - [14]Spermathecal diverticula: (0) absent, (1) 1, (2) 2, (3) 3, (4)>3,
 - [15]Spermathecal diverticula: (0) absent, (1) uniloculate, (2) multiloculate, (3) branched, (4) bifid,
 - [16]Spermathecal diverticula, length: (0) absent, (1)<ampulla+duct, (2) =ampulla+duct, (3) >ampulla+duct,
 - [17]Last hearts in segment: (0) 10, (1)11, (2)12, (3)13,
 - [18]Gizzard segment: (0) absent, (1) 5, (2) 6, (3) 7,
 - [19]Gizzard, development: (0) absent, (1) weak, (2) moderate, (3) strong,
 - [20]Calciferous glands extramural to oesophagus: (0) absent, (1) present,
 - [21]Intestinal origin:(0) 10, (1) 11, (2) 12, (3) 13, (4) 14, (5) 15, (6) 16, (7) 17, (8) 18, (9) 19,
 - [22]Nephridial bladders: (0) absent, (1) present,
 - [23]Nephridial diverticula: (0) absent, (1) present,
 - [24]Male funnels: (0) proandric, (1) holandric, (2) metandric,
 - [25]Seminal vesicles, segments: (0) 9,12, (1) 9,10,11,12, (2) 11,12, (3) 12, (4) 9,10,12, (5) absent, (6) 8,9,12, (7) 12,13, (8) 11,12,13, (9) 9,12,13,
 - [26]Prostate type: (0) tubular, (1) tubuloracemose, (2) racemose,
 - [27]Prostate, extent: (0) restricted to segment 18, (1) not restricted to 18,
 - [28]Penial setae: (0) absent, (1) present,
 - [29]Prostatic bursa: (0) absent, (1) present,
- Of these, character 8 was constant, and 24 was uninformative, neither therefore contributing to the phylogeny.

The input data matrix is presented in Fig. 17.

SEARCH OPTIONS

The analysis was performed using PAUP, version 3.0s, of Swofford (1993). Because of the inordinate time needed for branch and bound searching, the heuristic search option was

employed with the following search settings: addition sequence: simple; 1 tree(s) held at each step during stepwise addition; tree-bisection-reconnection (TBR) branch-swapping performed; MULPARS option in effect; steepest descent option not in effect; initial MAXTREES setting = 900; branches having maximum length zero collapsed to yield polytomies; topological constraints not enforced; trees unrooted; multi-state taxa interpreted as polymorphism.

A principle underlying the analysis was that of 'pattern cladism' in which a priori evolutionary assumptions are minimised. Accordingly, no attempt was made to establish transformation series, and polarity, for each character. Character states were often placed in purely arbitrary order and the characters were run "unordered". However, the plesiomorph condition was implied, and symplesiomorphic matching avoided, by employment of an outgroup. This was selected as the apparently relatively plesiomorphic taxon *Graliophilus georgei*.

RESULTS

Heuristic searching under these conditions resulted in 29 equally and most parsimonious trees: tree length = 213; consistency index (CI) = 0.521; homoplasy index (HI) = 0.714; excluding uninformative characters, CI = 0.420, HI = 0.717; retention index (RI) = 0.626; rescaled consistency index (RC) = 0.326. The 29 trees are summarized in Fig. 16.

DISCUSSION

In an 'intuitive' systematic study in the first part of this paper it has been concluded that the North Queensland species of *Diporochoaeta*, with *Fletcherodrilus*, form a monophyletic group, diagnosed *inter alia* by loss of accessory genital markings, and that this warrants separate generic status, as the new genus *Terrisswalkerius*. It has also been concluded that *Fletcherodrilus* represents an apomorphic clade (but not necessarily the sister-group) of this assemblage but that, at least for convenience, this should be retained as a separate genus. It has further been determined that the Bunya Mountains isolate of *Diporochoaeta* merits separate generic status, as *Hiatidrilus bunya*, and that *Cryptodrilus semicinctus* Fletcher, 1890, from Grafton, on the Clarence River, New South Wales, is congeneric with it. It was suspected that implementation of these conclusions would leave the residue of

Diporochoaeta as a paraphyletic entity requiring further resolution. It was also considered that if *Fletcherodrilus* were a terminal, apomorphic clade of the *Fletcherodrilus-Terrisswalkerius* assemblage, only this joint assemblage would be a monophyletic whole and that separation of *Fletcherodrilus* would render *Terrisswalkerius* paraphyletic.

The cladistic analysis was instigated to test these taxonomic decisions and to investigate wider relationships of the above genera with the other Perionychini. To this end, the New Zealand type-species of *Diporochoaeta*, *D. intermedia*, was included in the analysis, in addition to species of these genera, as were the type-species of every Australian perionychin genus. Some additional species were included in the analysis.

The phylogram resulting from the cladistic analysis (Fig. 16) allows discussion of the above systematic conclusions. The *Terrisswalkerius-Fletcherodrilus* assemblage is indeed a monophyletic entity, with *Fletcherodrilus* forming a terminal, monophyletic clade, and separation of *Fletcherodrilus* as a distinct genus is shown to result in a paraphyletic *Terrisswalkerius*. The assemblage is defined by the synapomorphy loss of accessory genital markings (and intestinal origin in XVII). *Fletcherodrilus* forms an apomorphic, terminal clade in which the spermathecal and male pores have united midventrally, the spermathecal condition being a homoplasy with *T. mcdonaldi*, and, less significantly, the seminal vesicles have come to occupy segments XI and XII. *F. sigillatus* and *F. menurus* have departed from the condition in the type-species, *F. unicus*, and all *Terrisswalkerius* species, in which accessory genital markings are apomorphically absent, by developing a distinctive type of pleated genital markings ventrally in the vicinity of the spermathecal pores.

A striking feature of the phylogram is that the type-species of *Diporochoaeta*, *D. intermedia*, is separated by other genera from those *Diporochoaeta* species here assigned to *Terrisswalkerius* and, indeed, from all other *Diporochoaeta* species included in the analysis. It is not suggested that this preliminary analysis gives a definitive phylogenetic placement for *D. intermedia*, but separation of *Terrisswalkerius* from *Diporochoaeta* s. strict. is clearly justified. However, the analysis suggests that *Perionychella* Michaelsen, 1907, as exemplified by its type-species, *P. dendyi* (Spencer, 1892b), is the sister-taxon of the *Terrisswalkerius-*

Fletcherodrilus assemblage, from which it differs notably in having developed racemose prostate glands. The unifying apomorphy between *Perionychella* and this assemblage, extension of the prostates through more than one segment, is, however, very tenuous and is of doubtful significance.

The phylogram separates the remaining perionychin genera from *Diporochoaeta* as typified by *D. intermedia*. It suggests that the genus *Perionychella*, currently subsumed in *Diporochoaeta*, is the sister-taxon of the *Terrisswalkerius-Fletcherodrilus* assemblage. It is not inconsistent with the generic status of the other perionychin genera, *Graliophilus*, *Heteroporodrilus*, *Paraplutellus*, *Perionychella*, *Pinguidrilus*, *Plutellus*, *Pseudoperichaeta*, *Simsia*, and *Woodwardiella*, but significant autapomorphies remain to be established for some of these. Where genera are not monotypic this will require inclusion of more than one species from each genus, a procedure beyond the scope of the present study.

The phylogram also supports the decision to place *Cryptodrilus semicinctus* Fletcher, 1890, with *Diporochoaeta bunya* Jamieson, 1976b, in the new genus *Hiatidrilus*, the two being united by the synapomorphic doubling of the spermathecal diverticula. However, *H. semicinctus* remains a very discrete perionychin in being metandric and having a saddle-shaped clitellum. *Hiatidrilus* forms a clade with *Woodwardiella callichaeta* and *Simsia tuberculata*, the type-species of their genera, and with *Diporochoaeta capensis*, on three tenuous characters, which are homoplastic with other species. These are location of the first dorsal pore in intersegmental furrow 5/6, supposed forward movement of the intestinal origin to XVI and the presence of penial setae. *Simsia* is defined, as when erected, by the multiloculate condition of the spermathecal diverticula which is unique for the species computed, and by three homoplastic characters, including the putative development of tubular, from tubuloracemose, prostates.

Separation of *Diporochoaeta kershawi*, *D. victoriae* and *D. (=Perionychella) mortoni* from *Diporochoaeta* s. strict. is supported by the phylogram (Fig. 16) and the generic status of these species requires further consideration. However, their inclusion, with *Pinguidrilus*, in a clade which includes basally *Heteroporodrilus*, *Plutellus* and *Paraplutellus*, is probably artefactual. The latter three genera have long been regarded, and I consider correctly, as a

homogenous entity in the very distinctive complex alternation of their nephropores and the strong development of their calciferous glands. *Pinguidrilus* has a unique apomorphy, within the taxa included in the analysis, of loss of spermathecal diverticula.

Within *Terrisswalkerius*, of which all known species are included in the cladistic analysis (Fig. 16), the most plesiomorphic species appears to be *T. blounti*, but this has undergone a major apomorphy in reduction of the spermathecae to a single segment, this being VIII. At the other extreme, *T. atavius*, is the most derived species and forms the sister-taxon of *Fletcherodrilus* with which its only notable synapomorphy is duplication of the spermathecal diverticulum. It shows no apomorphies over its ancestor which is shared with *T. grandis* and *T. terraereginae*. These two species are tenuously linked by the synapomorphies of location of male pores in setal lines *ab* and of the gizzard in segment V, both homoplastic conditions. Other pairs of sister-species are: *T. milliamillai* and *T. mcdonaldi* (as predicted in the systematics section), *T. athertonensis* and *T. oculatus*, *T. kuranda* and *T. canaliculatus*, and, again as suggested above, *T. nashi* and *T. liber*. Although the synapomorphies within each pair of species may seem of questionable significance, generation of the pairs in the context of the complete set of data and of the tree warrants serious consideration of the relationship indicated. The pairing of the undoubtedly extremely close if not conspecific *T. nashi* and *T. liber* gives substance to this argument. Whereas some species of *Terrisswalkerius* form paraphyletic series, within the *Terrisswalkerius* section of the *Terrisswalkerius-Fletcherodrilus* assemblage, a striking monophyletic species group is observable, consisting of *T. athertonensis*, *T. oculatus*, *T. canaliculatus*, *T. kuranda*, *T. crateris*, *T. nashi* and *T. liber*. For the same reasons this grouping deserves further consideration though it is based on only two, apparently weak synapomorphies, location of the first clitellar segment at XIII, and development of tubular, from tubuloracemose prostates, both of which are homoplastic states.

ACKNOWLEDGEMENTS

I am grateful to the collectors who are acknowledged in the text for making this paper possible and to the authorities and staff of the Queensland Museum for providing facilities for this work. This study is part of a survey of the Australian Megascolecidae carried out with Australian

Biological Resources Study financial support which is gratefully acknowledged. All illustrations are by the author

LITERATURE CITED

- BEDDARD, F.E. 1889. On the oligochaetous fauna of New Zealand with preliminary descriptions of new species. *Proceedings of the Zoological Society of London* 1889: 377-382.
1890. Observations upon an American species of Perichaeta and upon some other members of the genus. *Proceedings of the Zoological Society of London* 1890: 52-69.
- BEDDARD, F.E. 1895. 'A monograph of the order Oligochaeta'. Oxford: Clarendon Press.
- DYNE, G.R. & WALLACE, C.C. 1994. Biodiversity and conservation of the earthworm fauna of the wet tropics of Queensland's heritage area. *Memoirs of the Queensland Museum* 36 (1): 59-66.
- FLETCHER, J.J. 1886b. Notes on Australian earthworms—Part II. *Proceedings of the Linnean Society of New South Wales* 1 (2): 943-973.
- 1887a. Notes on Australian earthworms—Part III. *Proceedings of the Linnean Society of New South Wales* 2: 375-402.
1889. Notes on Australian earthworms—Part V. *Proceedings of the Linnean Society of New South Wales* 3 (2): 1521-1558.
1890. Notes on Australian earthworms—Part VI. *Proceedings of the Linnean Society of New South Wales* 4 (2): 987-1019.
- JAMIESON, B.G.M. 1970a. A revision of the Australian earthworm genus *Woodwardiella* with descriptions of two new genera (Megascolecidae: Oligochaeta). *Journal of Zoology, London* 162: 99-144.
- 1971b. Earthworms (Megascolecidae: Oligochaeta) from Western Australia and their zoogeography. *Journal of Zoology, London* 165: 471-504.
- 1971c. A review of the megascolecoid earthworm genera (Oligochaeta) of Australia. Part III - The subfamily Megascolecinae. *Memoirs of the Queensland Museum* 16 (1): 69-102.
- 1971d. Descriptions of the type-species of the earthworm genera *Plutellus* and *Digaster* (Megascolecidae: Oligochaeta). *Bulletin du Museum National d'Histoire Naturelle, Paris* 42: 1300-1310.
- 1972a. The Australian earthworm genus *Spenceriella* and description of the two new genera (Megascolecidae: Oligochaeta). *Memoirs of the National Museum of Victoria* 33: 73-87.
- 1972b. Further species of the Victorian earthworm genus *Simsia* Jamieson, 1971 (Megascolecidae: Oligochaeta) with a numerical analysis of intersetal ratios. *Memoirs of the National Museum of Victoria* 33: 89-108.
- 1974a. The indigenous earthworms (Oligochaeta: Megascolecidae) of Tasmania. *Bulletin of the British Museum (Natural History)* 26, 4: 203-328.
- 1976a. A re-examination of the type-species of *Diporochoeta* Beddard, 1890. (Megascolecidae: Oligochaeta). *Journal of the Royal Society of New Zealand* 6: 37-44.
- 1976b. The genus *Diporochoeta* (Megascolecidae: Oligochaeta) in Queensland. *Zoologische Verhandlungen* 149: 1-57.
- JAMIESON, B.G.M. & WAMPLER, J.E. 1979. Bioluminescent Australian earthworms. II. Taxonomy and preliminary report of the bioluminescence in the genera *Spenceriella*, *Fletcherodrilus* and *Pontodrilus* (Megascolecidae: Oligochaeta). *Australian Journal of Zoology* 27: 637-669.
- MICHAELSEN, W. 1891. Oligochaeten des Naturhistorischen Museums im Hamburg. *IV. Jahrbuch der Hamburgischen wissenschaftlichen Anstalten, Hamburg* 8: 3-42.
1900. 'Das Tierreich', Vermes, Lief. 10, Oligochaeta. (Friedlander: Berlin).
1916. Results of Dr. E. Mjoberg's Swedish Scientific Expedition to Australia 1910-1913. Oligochaeten. *Kungliga Svenska Vetenskapsakademiens Handlingar* 52 (13): 3-74.
- SPENCER, W.B. 1892b. Preliminary notice of Victorian earthworms. Part II. The genus *Perichaeta*. *Proceedings of the Royal Society of Victoria* 5: 1-26.
1900. Further descriptions of Australian earthworms, Part I. *Proceedings of the Royal Society of Victoria* 13 (n.s.) (1): 29-67.
- STEPHENSON, J. 1933. Oligochaeta from Australia, North Carolina, and other parts of the world. *Proceedings of the Zoological Society of London* 1932: 899-941.
- SWOFFORD, D. 1993. PAUP: Phylogenetic analysis using parsimony, version 3.0s. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.
- WALLACE, C.C. 1972. An examination of the classification of some Australian megascolecoid earthworms (Annelida: Oligochaeta) by numerical methods. *Memoirs of the Queensland Museum* 16 (2): 191-209.